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BIOLOGY AND ECOLOGY OF FALSE WIREWORMS IN SOUTH DAKOTA

(COLEOPTERA: TENEBRIONIDAE)

BY

CARROL OTTO CALKINS

A thesis submitted
in partial fulfillment of the requirements for the
degree Doctor of Philosophy, Major in
Entomology, South Dakota
State University

1973

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BIOLOGY AND ECOLOGY OF FALSE WIREWORMS IN SOUTH DAKOTA

(COLEOPTERA: TENEBRIONIDAE)

Abstract

CARROL OTTO CALKINS

Under the supervision of Dr. Vernon M. Kirk

False wireworms were important pests of wheat on the Great Plains during the early 20th century. Until recently, they were of little importance; however, they are now occasionally appearing in damaging proportions. The purpose of studying the biological and ecological aspects of these insects in South Dakota was to understand the factors responsible for their demise and the circumstances that could affect the recurrence of damaging populations.

The more common species of false wireworms found in South Dakota during this study were *Eleodes suturalis* (Say), *E. opaca* (Say), *E. hispilabris* (Say), *E. tricostata* (Say), *E. extricata* (Say), *E. obsoleta* (Say), and *Embaphion muricatum* Say.

The laboratory and field life history studies revealed that *Eleodes suturalis, E. opaca,* and *Embaphion muricatum* were potentially the most important false wireworm pests of wheat in South Dakota. Distribution of these species was closely correlated to well-drained elevated areas such as ridges and knolls. *Eleodes suturalis* was found most prevalent along the edges of fields, and *E. opaca* was distributed generally within the field but at some distance from the edge. Early workers described infestations of false wireworms as being restricted to light sandy soils, and this study substantiated this fact for

most species. However, *E. opaca* was found more abundantly in heavy clay soil types; *E. suturalis* was commonly found in clay, loam, and silt as well as in sandy soils; and *Embaphion muricatum* was observed nearly as often in loam soil areas as in sandy soils.

The deleterious effects of selenium (a component of clay soil in South Dakota) were not evident when the response of *Eleodes opaca* to it was measured. The growth rate of *E. hispilabris,* which is rarely found in clay soils, was affected by high levels of selenium. Thus, selenium was implicated as a factor in clay soils that may limit the distribution of certain false wireworm species in South Dakota.

Attempts to determine the economic threshold of *E. suturalis* by artificial infestation with laboratory-reared insects were generally unsuccessful. Populations necessary to substantially reduce yield were more than 10 times higher than naturally occurring damaging populations.

Food preferences of *E. suturalis* and *Embaphion muricatum* revealed that both species fed readily on seeds of most crop plants, and that the seeds of introduced plants were more severely damaged than those of native grasses. Seeds of some species were not attacked before germination, but as these seeds germinated, they became very susceptible to attack.

Eleodes suturalis, E. opaca, E. hispilabris, E. extricata, E. obsoleta, and *Embaphion muricatum* were successfully mas reared in the laboratory, and several cultures of these insects have been provided to scientists in the United States and England.

The life cycles of all species studied extended into 2 cropping seasons. If wheat was not grown on the same ground in consecutive years, the life cycle of these insects would be broken. This cropping sequence is interrupted by a cultural practice referred to as summer-fallowing. The result has been a prevention of high populations developing within fields. As crop prices, land value, and taxes rise, there is a tendency for growers to forego this cultural practice and to grow wheat continuously in the same field. The result in recent years has been an increase in damage by false wireworms. Because of the economic and agronomic changes presently occurring, this group of insects could again become very important in the growth of wheat.

BIOLOGY AND ECOLOGY OF FALSE WIREWORMS IN SOUTH DAKOTA

(COLEOPTERA: TENEBRIONIDAE)

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Doctor of Philosophy, and is acceptable as meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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This investigation was conducted during my employment as an entomologist at the Northern Grain Insects Research Laboratory and was supported by that facility.

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INTRODUCTION

False wireworm is the common name for larvae of beetles of the genera Eleodes and Embaphion. They belong to an extensive coleopterous family, Tenebrionidae, which has a total of 1440 described species and subspecies of which 210 belong to the genus Eleodes (Tanner 1961) and 7 belong to the genus Embaphion (Blaisdell 1909). The common name is derived from the fact that the larvae closely resemble larvae of Elateridae, the true wireworms. False wireworm larvae can be distinguished from true wireworm larvae by several taxonomic characteristics (St. George 1925). However, the easiest methods for field identification of false wireworms include: longer and more prominent legs, longer antennae that are conspicuously clavate, the body not being flattened, and more rapid movement of the larvae (Hyslop 1912).

False wireworms are generally described as inhabiting the arid and semi-arid portions of the United Stated west of the 97th meridian. No records have been found of collections east of the Mississippi River (Tanner 1961). These beetles occupy the ecological niche in arid regions which is usually held by the Carabidae in more humid regions (Borror and DeLong 1955). The larvae, for the most part, exist below the soil surface where they feed on seeds, roots, and decaying organic matter of various kinds. The adults are usually crepuscular or nocturnal seeking shelter during the day under litter, rocks, dried animal dung, and in small animal burrows. They feed on seeds, plant leaves, chaff, and occasionally soft bodied insects (Webster 1912).

Because this is not a taxonomic problem, I will not stress the details of the original and subsequent descriptions and name changes. Horn (1870) described the adults of all species that have been found in South Dakota. Blaisdell (1909) presented detailed morphological and sexual dimorphism descriptions of all species for taxonomic purposes. Tanner (1961) described the distinguishing characteristics of the genus *Eleodes.* His key to the species is still unfinished because the study of the genitalia of several rare species is incomplete. However, his checklist and descriptions do not alter the species names given by Horn 79 years previously.

Tanner's characterization of Eleodini is as follows: the front and middle tarsi are 5-jointed; the hind tarsi are 4-jointed; the anterior coxal cavities are closed behind; the ventral abdominal segments are 5, in part connate; the tarsal claws are simple, the penultimate joint of the tarsi are not spongy beneath. Wickham (1890) gave detailed descriptions of the genus *Embaphion* as well as of the species *E. muricatum.*

St. George (1925) and Boving and Craighead (1930) have presented descriptions and drawings of the larvae of several species. Therefore, it was not necessary for me to repeat their work in devising larval keys for identification.

Extensive surveys throughout South Dakota revealed that 6 species of *Eleodes,* 1 species of *Embaphion,* 1 species of *Glyptasida,* and 2 species of *Asidopsis* were present. The species involved were identified by T. J. Spilman of the United States National Museum in

Washington, D.C. A reference collection identified by him is maintained at the Northern Grain Insects Research Laboratory, Brookings, S. Dak., and was used for subsequent identifications during this study. According to C. A. Triplehorn, Ohio State University, Columbus, the correct names for the species found in South Dakota are as follows:

Eleodes suturalis (Say)
Eleodes opaca (Say)
Eleodes hispilabris (Say)
Eleodes tricostata (Say)
Eleodes extricata (Say)
Eleodes obsoleta (Say)
Embaphion muricatum Say
Glyptasida sordida (LeConte)
Asidopsis opaca (Say)
Asidopsis polita (Say)

Glyptasida sordida, A. opaca, and *A. polita* were found only in certain restricted areas of the state and usually so infrequently that they were included only in the distribution aspects on the Great Plains in this dissertation.

False wireworms were extremely important pests of wheat during the early 20th century. Several publications describing damage and control appeared in the scientific literature before 1930. Since that time, references to damage and control of false wireworms were very scarce. Several elements have changed which have resulted in a reduction in the importance of these insects as pests. The purpose of this study of the biological and ecological aspects of these insects in South Dakota was to understand the factors responsible for their demise. By recognizing these factors, it becomes possible for workers to predict the circumstances which could cause a recurrence of the destructiveness of these insects, as well as being cognizant of the proper means of avoiding or controlling such damage.

The biologies of some of the species found in South Dakota have been worked on extensively, but not much attention has been given to the others. Much of the information necessary for use in life table studies or for computer modeling has not been determined or properly categorized. Although this dissertation does not attempt to develop computer models, the biological information derived from these experiments and from the literature is placed in a form from which these life tables and computer programs can be derived.

The literature generally describes the distribution of these insects as being closely related to light or sandy soils. However, false wireworm damage occurs in regions of clay, silt, and loam soils in South Dakota frequently enough to cast doubt on this contention. The local distribution of false wireworm beetles has always been described in association with straw stacks, grain shocks, and accumulations of Russian thistles along field edges, all of which are products of earlier agricultural practices. Distribution and movement of adults have not been determined on an individual field basis since the advent of combine harvesting and the use of herbicides. The knowledge of such distribution and movement of ovipositing females allows insight into larval distributions and damage patterns.

The lists of food plants for these insects are quite extensive, but no quantitative comparison of food preferences has been made for any species. Therefore, this aspect was also investigated.

Experimentation involving the biologies of these species necessitated a program of growth and maintenance in the laboratory. The techniques involved in this program were the 1st step toward initiating mass rearing procedures. Matteson (1966a, 1966b) demonstrated the ease of rearing *Eleodes suturalis* in large numbers, and many of his techniques were used to explore the potential for mass rearing other species in the laboratory.

CHAPTER I

BIOLOGY AND LIFE HISTORY OF THE EXPERIMENTAL INSECTS

During the course of the present investigation, extensive laboratory and field studies were conducted to determine the basic elements of the biology of these insects. Detailed aspects of the biology such as the length of the life stages (egg, larva, prepupa, pupa, and adult) as well as egg measurements, larval instar determinations, and rates of oviposition are most easily and accurately determined under controlled conditions in the laboratory. However, seasonal appearances of the various life stages are more accurately obtained by close observations and detailed sampling in the field.

By observing the seasonal appearance of one or more life stages in the field and being aware of the duration of all of the life stages, it becomes possible to construct a complete life history of a species and to understand and predict when each stage would be expected to occur. By knowing the biotic potential of each species, the length of the life cycles, and the mortality factors involved, detailed life tables can be constructed. When the effects of various environmental parameters are included, computer models of the population dynamics of each species can be developed and population fluctuations can be predicted whenever climatic and agricultural changes occur. The construction of such life tables and computer models is beyond the scope of this study, but the information on the basic biology of each species is of the type necessary for these more sophisticated approaches.

Literature Review

Eleodes suturalis: Complete taxonomic and morphological descriptions of all stages of this species were given by Wade and St. George (1923). They also gave a fairly complete resume of its life history. This species overwinters in southern Kansas as adults under straw, grass, weeds, and refuse and also as larvae of various sizes deep in the soil. The adults emerge in early spring and lay eggs in the soil throughout the summer and fall. The eggs are deposited ca. 3/4-1 in. deep in loose soil, frequently in groups of 10-60. The egg is described as being elliptic-cylindrical, ca. 1.5-2 mm in length, and 1 mm in width. It is opaque ivory white with a smooth surface. The incubation period in the field is 8-10 days but varies according to moisture and temperature regimes.

Recently hatched larvae are semiopaque white and average 2.5 mm in length and ca. 0.3 mm in width. These proportions vary little throughout the larval life. The greatest period of growth occurs during the 1st 3 or 4 weeks after which growth slows considerably. Wade and St. George (1923) found 6 instars, but they had some difficulty in determining the exact number. Where adequate food was available, the larvae reached maturity in ca. 110-130 days. Many larvae in the field reached the 4th or 5th instar during late fall and overwintered in that condition. They resumed feeding in March until mature and then entered a semiquiescent prepupal stage for 4-10 days. The pupal stage occurred in earthen cells ca. 3 in. deep in the soil and lasted 10-22 days.

Upon emerging from the pupal cells, the adults were inactive for a short time while the exoskeleton hardened. Mating occurred 6-7 days after emergence and the 1st eggs were deposited 20-22 days thereafter. The average number of eggs deposited by a series of 100 females was 108, while the maximum number deposited by a single female was 335. The life expectancy of adults exceeded 2 years in the field.

Matteson (1966a) reported that the eggs were somewhat smaller (1.2-1.37 mm long and 0.63-0.77 mm wide) than those measured by Wade and St. George. The females deposited ca. 14-20 eggs/day. Using close observations and applying Dyar's Law (Dyar 1890), Matteson established that 11 instars normally developed under his rearing conditions. The larval period, from 1st to 10th instar, lasted 40-50 days at 80°F. During the 10th instar, the larvae required an exposure to cold temperatures of at least 60 days to break diapause and permit pupation to occur. After being returned to warmer temperatures, the larvae molted once more, constructed earthen cells, and entered the prepupal stage after which the insects pupated for 14-21 days.

Eleodes opaca: There was only 1 generation per year observed by Swenk (1923). Adults were commonly found in the field from mid-June to mid-September and reached their greatest abundance in eastern Nebraska during late July and in western Nebraska ca. 15 days later. These beetles usually lived for 2-3 months, but occasionally survived as long as 4 months. Adults began mating 4-6 weeks after emerging from the pupal cell. Oviposition occurred a few days later and the oviposition period lasted from 2 to 8 weeks. The total number of eggs laid by each female varied from 25 to 400 but averaged ca. 100. Eggs were deposited from early July to October, but mostly during August (Swenk 1923).

McColloch (1919) reported that the number of eggs each female produced per day during the period of egg laying ranged from 2 to 8 and averaged 5.3. The maximum number of eggs per day laid by each of 6 females ranged from 6 to 34.

The eggs were described by McColloch (1919) as being oval in shape longitudinally and circular in diam. The dimensions ranged from 1.1 to 1.4 mm in length and 0.50 to 0.65 in width. A sticky secretion covered the egg, causing particles to adhere to it when deposited. The incubation period varied with temperature; eggs deposited in midsummer hatched in 6-10 days while those deposited in the fall took up to 19 days to hatch. Swenk (1909) described the egg as ovaliform, unsculptured, glistening white when 1st laid but changing to a creamy yellow before hatching. The size ranged from 1.5 to 1.7 mm long by 0.8 to 0.85 mm wide. He observed the same incubation periods as McColloch.

On hatching, the larvae were 2.8 mm in length. Growth in the early stages was very rapid. The larvae apparently had 11 instars, and the average time spent in the larval stage was 318 days (McColloch 1919). However, this included the 199-day overwinter resting period spent in the 10th instar. Swenk (1923) also observed 11 instars but reported that the overwintering stage is the 9th instar and the larvae molt twice in the spring before pupating. Both authors agreed that the prepupal stage lasted 7 days. McColloch (1919) indicated that the pupae varied from 13 to 15.5 mm in length and from 3.5 to 5.5 mm in width. They were white with semitranslucent appendages, but with development the color changed to creamy yellow with reddish brown appendages. The pupal stage required from 9.6 to 20.6 days to complete. The pupal stage, as observed by Swenk (1909), ranged from 11 to 12 days, but he later reported (1923) that this stage lasted 8 to 20 days. Pupation began in western Nebraska ca. mid-May. Pupae were commonly found during May, June, and July in most years.

Eleodes hispilabris: Adults were found to overwinter almost entirely in waste areas, often being found in burrows of small mammals (Wakeland 1923). Eggs were deposited singly at depths of 1/2-2 in. in loose soil during the latter part of May and the 1st part of June. Haverfield (1965) observed females depositing their eggs by inserting the posterior portion of their abdomen into loose, soft soil. The eggs were described as being ca. 1.5 mm in length, smooth, white, and round to slightly oblong. The eggs were coated with a sticky substance that caused soil particles to adhere to them, thus rendering them almost impossible to find in the soil. The eggs hatched in 9-13 days (Haverfield 1965). Wakeland (1923) reported that the incubation period averaged 14.91 days.

The newly hatched, semiopaque white larvae seemed to require a resting period after hatching before feeding began. According to Haverfield (1965), the number of instars depended upon temperature, moisture, and food abundance. He found 6-8 instars while Wakeland

(1926), rearing 92 larvae singly, observed 11 instars. The larval period ranged from 302 to 644 days and averaged 369.19 days. The 6th instar alone lasted ca. 104 days. The pupal stage required 33.59 days. Haverfield (1965) observed a prepupal period that lasted 4-6 days, and found that the pupal stage required only 15 to 20 days.

Wakeland (1922, 1923, 1926) found that adults began emerging from pupal cells ca. August 1 and lived until June of the following year. They began laying eggs during April and May and continued until their death. Larvae that hatched in June fed and developed throughout the summer and became nearly full grown by fall. They overwintered in this stage and pupated during July. Thus, 2 generations overwintered simultaneously, one in the larval stage and the other as an adult. Haverfield (1965) also observed larvae and adults overwintering.

Eleodes tricostata: McColloch (1918) found that the eggs of this species were deposited by females in the field from mid-July to mid-November. They were bluntly oval longitudinally, circular in diam, and varied in length from 2.2 to 2.5 and were ca. 1.2 mm in width. When deposited, they were coated with a sticky solution that caused soil particles to adhere to them. The average number of eggs per female was 176 with extremes of 103 and 262. The largest number of eggs deposited by a single female in 24 hr was 51. The period of oviposition was 48.8 days with extremes of 24 and 75. An average of 3.7 eggs/female per day was produced. The incubation period varied with temperature: 6-11 days were required in July and August and as much as 46 days in November.

The larvae were creamy white when 1st hatched, but after the 1st molt they changed to black; this color then persisted during the rest of the stage. The larval period ranged from 68 to 332 days but averaged ca. 280 days. The winter was passed in the next to last larval stadium. Larvae were found in the soil from July to May. At Manhattan, Kansas, the larvae appeared to be confined to native grassland. The prepupal period lasted from 5 to 10 days. The pupal stage ranged from 11 to 45 days but the average time was 18.45 days. Pupae were found from late May to late June. Adults began emerging in late June. No preoviposition period was observed, but oviposition occurred 3 days after copulation.

The adults lived up to 13 months, with the longest recorded period being 391 days. They were found in the field throughout the summer and fall and a few apparently overwintered. However, McColloch was never able to obtain eggs from overwintered beetles. Females seemed to outlive males.

Eleodes extricata: Adults of this species were present in the field from June to May (Wakeland 1926). No egg size was determined, but the incubation period ranged from 10 to 15 days and averaged 10.9 days. Eleven larval instars were detected. The duration of the larval period ranged from 344 to 448 days and averaged ca. 367 days.

No information about the prepupal period was available. The duration of the pupal stage ranged from 7 to 21 days and averaged 11.4 days. The occurrence of pupae was confined to June and July.

Matteson (1966b) observed that the pupal stage lasted from 14 to 17 days. No information was available about the seasonal occurrence or life expectancy of adults.

Eleodes obsoleta: Blumberg (1961) found that the adults of this insect lived only from early August to late October. The eggs were laid during August, September, and October and overwintered as such. He hypothesized that the larval stage began in May and ended in early June, and the pupae were present from June until August in Colorado. He did not observe any stage but the adult in the field and was not able to rear the insect successfully in the laboratory. Therefore, his conclusions for the life cycle are only based upon the seasonal appearance of the adults and the fact that larval forms appeared briefly in the laboratory at the end of May.

Embaphion muricatum: Wade and Boving (1921) gave complete taxonomic and morphological descriptions of each stage. They found that the egg size was variable, being 1.1-1.3 by 0.60-0.62 mm. The color was pure white when 1st deposited but changed to yellowish brown before hatching. The eggs were deposited during May and June in loose soil 1/2-1 in. deep, sometimes singly, but more often in clusters of 2-12. The average period of incubation was 10 days at temperatures of 80-90°F, but took 13 days at 70°F.

The length of the larval stage ranged from 76 to 96 days. Under field conditions, many larvae appeared to become nearly mature during late fall and overwintered in that form. The semidormant prepupal period which occurred in April lasted ca. 7-9 days. The pupal stage

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during May required 18-20 days. The pupae were pinkish white just after transformation but changed to a light yellow as development proceeded.

Adults did not mate until a week or more after emergence. The preovipositional period and rates of oviposition were not determined. Because adults may also overwinter, it appeared from the information supplied by Wade and Boving that they normally live up to 12 months in the field.

Laboratory Investigations

Materials and Methods

The essential aspects of false wireworm biology, such as size of egg, incubation time, number of larval instars, length of larval, prepupal, and pupal stages, and the rate of oviposition for each species were determined by using the same standardized methods. Certain biological aspects of some species required modification of these standard techniques; however, all alterations are described for the species involved.

Adults of each species were collected throughout western South Dakota. These adults of unknown age were brought to the laboratory for biological studies and for establishment of laboratory colonies. The separation of male and female beetles of each species was achieved by the use of criteria taken from Blaisdell (1909) and condensed into Table 1.

Table 1.--Distinguishing characteristics separating male and female false wireworm adults (Blaisdell 1909).

Species	Sexual characters: Male	Sexual characters: Female
Eleodes suturalis	Prothoracic femora with acute tooth 1/4 distance from apex.	Prothoracic femora with a small obtuse tooth.
E. opaca	Body moderately narrow and fusiform.	Body broadly fusiform oval.
	Abdomen moderately convex, impressed on 1st segment between coxae, slightly oblique to the intercoxal process and sterna.	Abdomen strongly convex.
	1st 2 joints at prothoracic tarsi slightly widened and clothed beneath with dense pads of spongy pubescence, surface of pads flat.	Prothoracic tarsi unmodified.
E. hispilabris	Prothoracic femora with an acute tooth at outer 1/3.	Prothoracic femora with an obtuse tooth at outer 1/3.
E. tricostata	Body oblong, oval, somewhat elongate.	Body oblong, robust.
	Antennae reaching to posterior 1/5 of prothorax.	Antennae reaching to posterior 1/4 of prothorax.
	Elytra widest at base.	Elytra widest at middle.
	Abdomen distinctly impressed at base of 1st segment and between the coxae.	Abdomen strongly convex.

Table 1.--Continued.

Species	Sexual characters: Male	Sexual characters: Female
E. tricostata (continued)	Anterior spur of prothoracic tibia 1/2-1/3 longer than posterior, gradually tapering from base to apex, and acute.	Anterior spur of prothoracic tibia 2 times as long as posterior, curved, distinctly broadened, with sides parallel, somewhat narrowing toward tip.
	1st joint of each prothoracic tarsus with a small, subacute tuft of yellowish pubescence on the produced tip beneath.	1st joint of prothoracic tarsus with a tuft of ordinary piceous spinules on the thickened tip.
	2nd joint of prothoracic tarsus slightly thickened at tip beneath with a similar and rather inconspicuous tuft; groove interrupted.	2nd joint of prothoracic tarsus unmodified.
E. extricata	Body fusiform-ovate, elongate.	Body ovate, rather robust.
	Antennae reaching just beyond base of prothorax.	Antennae reaching to base of prothorax.
	Elytra distinctly and gradually narrowed behind.	Elytra moderately narrowing from posterior 1/4.
	Abdomen slightly oblique, moderately convex, 1st segment flattened at middle, with intercoxal region concave.	Abdomen horizontal, strongly convex, intercoxal process convex.
	Prothoracic femora armed with subacute tooth.	Prothoracic femora unarmed.

Table 1.--Continued.

Species	Sexual characters: Male	Sexual characters: Female
E. extricata (continued)	1st joint of prothoracic tarsi clothed at tip beneath, with a small subtruncate tuft of golden pubescence usually darkly discolored.	1st joint of prothoracic tarsi narrowly and transversely thickened at tip beneath with short piceous spinules.
	Tip not very thickened, groove interrupted.	Groove interrupted at ventral apical margin.
E. obsoleta	Body elongate.	Body robust.
	Elytra gradually narrowed posteriorly, quite evenly and arcuately declivous behind.	Elytra broady oval and slightly narrowed posteriorly, usually arcuately and rather vertically declivous behind.
	Abdomen moderately oblique, not strongly convex, feebly impressed at middle of 1st 2 segments, intercoxal process somewhat concave.	Abdomen horizontal and strongly convex.
	Anterior spurs of prothoracic tibia ca. twice as long as posterior, slightly curved, feebly widened and gradually narrowed from base to apex.	Anterior spurs of prothoracic tibia usually ca. 1/3-1/2 longer than posterior, moderately curved and gradually narrowed from base to apex, noticeably widened.
	1st joint of prothoracic tarsi with minute tuft of modified spinules scarsely evident, ordinary spinules present on thickened tip beneath.	1st joint of prothoracic tarsi with ordinary spinules on thickened tip beneath.

Table 1.--Continued.

Species	Sexual characters	
	Male	Female
Embaphion muricatum	Abdomen moderately convex and not noticeably impressed.	Abdomen rather strongly convex.
	Prothoracic tibia quite suddenly and briefly constricted at base.	Protibia gradually narrowed at base.

Eggs were collected and an ocular micrometer was used to measure eggs of all species. To determine the fecundity of the females, adults were confined to aluminum pans (15X10X7.6 cm) with ca. 4 mm of damp sand that was previously sifted so that all particles were smaller than the eggs. Five females and 2 males were included in each of 10 pans that were then covered to maintain a high humidity, thus preventing desiccation of the eggs. Each adult was fed ca. 2 kernels of wheat a day. Eggs were separated from the sand by washing the sand through a No. 35 sieve (U.S. Standard, 500 M) that retained the eggs. The eggs were then washed from the sieve onto a filter paper in a Buchner funnel under vacuum. The eggs adhering to the filter paper were counted, placed into petri dishes (100X15 mm), and incubated at 24-28°C until they hatched. The percentage of eggs that successfully hatched and the incubation time were determined.

The number of larval instars was determined from head capsule measurements with an ocular micrometer. The head capsules of newly hatched larvae were measured and the larvae were placed in small (60X20 mm) petri dishes containing ground wheat. The dishes were placed in plastic bags containing moist paper towels to prevent desiccation of the larvae and were held at constant temperatures of 21-24°C. Larval head capsules were measured daily and the ground media was examined for exuvia to determine the number of instars. Dyar's Law was applied to assure that all instars were accounted for.

Pupation sites were provided in the same type of pans that were used for oviposition. Mature larvae and prepupae were placed in moist, sandy soil within the pans and held in cabinets at 24-27°C and 90-100% RH. The pans were examined daily for adult emergence.

Newly emerged adults were placed in oviposition containers to determine the length of the preoviposition period. The oviposition media was examined daily for the presence of eggs.

Results and Discussion

My laboratory data and the vital statistics established by other workers for each species are summarized in Table 2. Cited data is followed by a letter indicating the reference citation. These combined statistics encompass almost all of the pertinent details relating to the life cycles of these 7 species of false wireworms. In many instances, I have repeated experiments that were previously done by someone else. In other cases, I did not repeat certain aspects; for example, J. W. Matteson's work preceded the initiation of my work by only 1 year. We used the same laboratory and about the same technical personnel and equipment. Other experiments were unsuccessful due to such limitations as an inadequate supply of insects. All pertinent laboratory data are discussed for each species.

Eleodes suturalis: The eggs are bluntly oval in shape with a milky white smooth surface. Egg measurements based upon 30 observations ranged from 1.20 to 1.33 by 0.68 to 0.76 mm; this was well within the range found by Matteson (1966) but smaller than eggs measured by Wade and St. George (1923). The percentage of eggs that hatched and the periods of incubation at various temperatures are shown in Table 2. The highest percentage of eggs to hatch (82%)

Table 2.--Laboratory biology of false wireworms found in South Dakota.

Species	Egg: Size range (LxW, mm)	Egg: % hatch	Egg: Incubation period (days)
Eleodes suturalis	1.20-1.33X0.68-0.76 1.5 -2 X 1[h] 1.2 -1.37X0.63-0.77[b]	75 (30°C) 62 (25°C) 82 (20°C) 62 (15°C) 0 (10°C)	7.47 7.81 12.22 26.19 - 8-10[h]
E. opaca	1.20-1.32X0.65-0.73 1.1 -1.4X0.50-0.65[d] 1.5 -1.7X8-0.85[e]	75-85	- 6-9 6-19[d] 6-10[f]
E. hispilabris	1.10-1.32X0.65-0.75 1.5[a]	47.2	10-12 9-13[a] 14.91[i] 10-18[i]
E. tricostata	2.0-2.91X1.1-2.0 2.2-2.5X1.2[c]	50.0	10 14.5 Av[c] 6-11 Aug[c] 46 Nov[c]
E. extricata	0.9-1.4X0.60-0.75	65 (29°C) 55 (24°C) 0 (18°C) 0 (13°C)	8 10 10.86[i]
E. obsoleta	1.7-2.3X0.98-1.33		8
Embaphion muricatum	1.20-1.35X0.65-0.78 1.1-1.3X0.60-0.62[g]	81-98 (29°C) (21°C)	4-9 10[g] 13[g]

Larva		Prepupa	Pupa
No. instars	Larval period (days)	Prepupal period (days)	Pupal period (days)
6[h]/ 11[b]/	120 110-130[h]/ 40-50[b]/	6 4-10[h]/	17 10-22[h]/ 14-21[b]/
12 11[d]/ 11[f]/	60-80 300-350[f]/	6 7[f]/	9.6-20.6[d]/ 11-12[e]/ 8-20[f]/
6-8[a]/ 11[i]/	369[i]/	4-8 4-6[a]/	10 33.59[i]/ 13-79[i]/ 15-20[a]/
Unknown	280[c]/	5-10[c]/	18.45[c]/
11[i]/	79-96 367[i]/	14	14-17[b]/ 11.4m[i]/
9 (8-10)	151.7	6.8	19.9
14 (11-16)	76 79[g]/	4 7-9[g]/	13.4 18-20[g]/

Table 2.--Continued.

Species	Adult: Preovi-position period (days)	Total no. eggs	No. eggs/♀ per day	Total adult life
Eleodes suturalis	26-29[h]	108 av[h] 335 max[h]	29.13 14-20[b]	2-3 yr[h]
E. opaca	10-20[d] 28-42[f]	389+[d] 25-400[f]	5.3[d] 7-8[f]	3-3.5 mo 2-4 mo[d] 2-3 mo[f]
E. hispilabris	3-4 wk 8-9 mo[i]	Unknown	17.7	1 yr 10 mo[i] 8-16 mo[i]
E. tricostata	Unknown	176 av[c]	2.0 3.7[c]	3-4 mo 11-13 mo[c]
E. extricata	21	Unknown	3.47	2 mo
E. obsoleta	Unknown	Unknown	2-4	2 mo
Embaphion muricatum	10-14	230+	5.36	3-4 mo

a/ Haverfield (1965)
b/ Matteson (1966a, 1966b)
c/ McColloch (1918)
d/ McColloch (1919)
e/ Swenk (1909)
f/ Swenk (1923)
g/ Wade and Boving (1921)
h/ Wade and St. George (1923)
i/ Wakeland (1926)

was at 20°C. The incubation period ranged from 7.5 to 26.0 days at temperatures of 30-15°C.

Because the number of larval instars (11) was established by Matteson (1966a, 1966b), I did not repeat this work. However, frequent examination and head capsule measurements for selection of larvae for use in other experiments did not refute his findings. The majority of larvae reared in colonies of ca. 200 individuals took ca. 120 days to complete development. An additional 60 days were spent in a cold treatment (4°C) to break diapause. A few individuals completed their development in 40-50 days as reported by Matteson (1966a, 1966b) but these were the exceptions rather than the rule.

During the last instar, larvae became quite lethargic and ceased to feed after removal from the cold treatment. A noticeable change in appearance took place as they became shorter and thicker in diam. This prepupal stage was found to last ca. 6 days at 27°C. Just prior to entering this stage, the larva formed an earthen cell by bending and turning in place; this resulted in a cavity being formed that was ca. 3-4 times the volume of the larva.

The pupal stage lasted from 10 to 22 days after which the adult emerged from the earthen cell. The exoskeleton of the teneral adult was still soft and pale brown. It gradually hardened and became black with the characteristic reddish brown stripe along the medial elytral line.

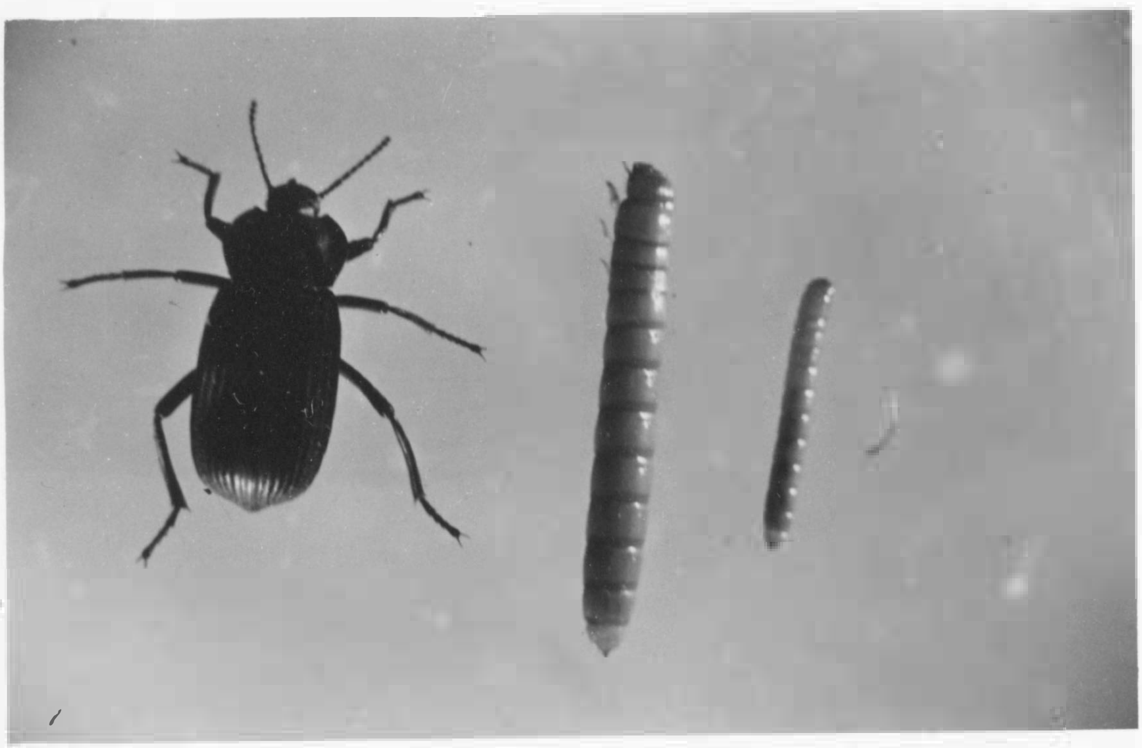
The adult was not reproductively mature for some time after it emerged. Mating started 6-7 days after emergence and oviposition began 20-22 days thereafter. The average daily rate of oviposition per female for a period of several weeks was 29.19 eggs. The life expectancy of adults in the laboratory seldom exceeded 1 year; however, they were held at constant warm temperatures and high humidities and were not subjected to overwintering conditions which might have prolonged their life. Figure 1 illustrates the relative sizes and shapes of the adult, and the 9th, 5th, and 2nd instars.

Eleodes opaca: The eggs closely resembled eggs of the other species of *Eleodes* in that they were oval and milky white when laid and turned creamy yellow just before hatching. Measurements of 74 eggs ranged from 1.2 to 1.32 mm in length, 0.65 to 0.73 mm in width; these were smaller than Swenk's determinations (1909) but only slightly different from McColloch's (1919). The percentage of eggs that hatched at 24°C was 75-85%. The incubation time ranged from 6 to 9 days at that temperature; this was fairly close to that observed by McColloch (1919) and Swenk (1923).

Some difficulty was experienced in rearing larvae of *E. opaca* on ground wheat in the absence of soil. Only 5 instars were completed under these conditions (Table 3). Other head capsule measurements were made on individuals taken from the laboratory colony for use in other experiments. By using Dyar's Law to determine what instars were missed in our examinations, it appeared that this species had 12 instars and that instars 6, 7, and 8 were not observed.

The larvae took from 60 to 80 days to complete development in soil in rearing containers. No data were accumulated for prepupal, pupal, or preovipositional periods.

Fig. 1. Adult and 9th-, 5th-, and 2nd-stage larvae of *E. suturalis*.



Adults lived more than 2 months in the field as determined by mark and recapture techniques; however, field-collected adults rarely survived longer than 1 month in the laboratory.

Eleodes hispilabris: The eggs of this species were quite similar in appearance to other species covered in this study. The egg dimensions ranged from 1.10 to 1.32 by 0.65 to 0.75 mm for 111 observations. Only 47.2% of the eggs hatched at 24°C and 90-100% RH. The incubation period was 10-12 days at 24°C.

Difficulty was encountered in rearing larvae in petri dishes on ground wheat where the number of molts could be detected easily. Therefore, it became necessary to remove larvae from soil periodically to measure head capsules. The head capsule width measurements tended to cluster around certain means. When ratios of adjacent means were calculated, the ratios were relatively constant. This agreed with calculations proposed by Dyar (1890) to detect all larval instars of lepidopterous larvae. This species appeared to have 13 instars (Table 4). Larvae in rearing containers developed from egg to the 12th instar in ca. 4 months. At that time, they seemed to require a cold treatment of 2 months similar to that reported by Matteson (1966a, 1966b) for E. suturalis. Occasionally, when transferring mature larvae to fresh soil in preparation for placing them in the cold room, a pupa would be discovered which led to doubts about an obligatory diapause. To determine whether these larvae had an obligatory diapause or merely a facultative one, pans containing ca. 200 mature larvae were periodically kept at 27°C for an additional

Table 4.--Number of instars based upon average head capsule measurements and growth ratios of larvae of E. hispilabris.

Instar	No. measured	Av head capsule width (mm) Mean	Range	Growth ratio
1	40	0.398	0.373-0.433	
2	2	.467	--	1.17
3	18	.598	.543- .633	1.28
4	5	.736	.717- .767	1.23
5	1	.847 1/	--	1.15
6	1	1.020 1/	--	1.20
7	31	1.207	1.100-1.267	1.18
8	124	1.435	1.300-1.567	1.19
9	105	1.707	1.600-1.833	1.19
10	166	2.096	1.670-2.200	1.23
11	46	2.453	2.200-2.733	1.17
12	25	2.872	2.800-3.067	1.17
13	5	3.430	3.200-3.900	1.19

1/ Calculate means.

2 months to determine if all larvae would pupate. About 5% of all larvae entered the pupal stage without undergoing a cold treatment.

When larvae were returned to 27°C after being at 4°C for 60 days, they molted once more and entered the prepupal stage. This stage lasted 4-8 days. The pupal stage required ca. 10 days.

Adults did not begin laying eggs until 3-4 weeks after they emerged from the pupal stage. Their egg production was low initially and began to increase shortly thereafter. When at their peak, the number of eggs deposited by each female was 17.7 per day. The total number of eggs produced during an average adult lifetime was not determined; however, females appeared to continue laying eggs throughout most of their life. The life expectancy of both laboratory-reared and field-collected adults was ca. 1 year in the laboratory.

Eleodes tricostata: The eggs of this species were more yellowish than eggs of other species. The measurements taken from 111 eggs ranged from 2.0 to 2.91 by 1.1 to 2.0 mm, which is considerably larger than for the eggs of the other 6 species. The incubation period was 10 days at ca. 24°C. Only ca. 50% of the eggs hatched under those conditions. Considerable trouble was experienced in rearing the larvae. No larvae lived for more than a few days on ground wheat, and no large larvae were produced in soil in the colony rearing room.

The number of eggs produced by field-collected adults averaged ca. 2/day. Adults collected in the field lived from 3 to 4 months in the laboratory.

Eleodes extricata: The eggs of this species resembled eggs of most of the other species in size and appearance. The measurements taken from 131 eggs ranged from 0.9 to 1.4 by 0.6 to 0.75 mm. The incubation time at 29°C was 8 days while it took 10 days at 24°C. The percentage hatch was 65 and 55, respectively, for the 2 temperatures.

The larvae did not grow or develop well on ground wheat: they were only maintained until the 5th instar (Table 5). They did quite well in soil; however, the number of instars could not be determined

Table 5.--Average head capsule measurements, growth rates, and growth ratios of *E. extricata*.

Instar	Av head capsule width (mm)	Growth ratio	Av duration (days)
1	0.394		2.09
2	.428	1.09	5.88
3	.502	1.17	5.67
4	.600	1.19	5.20
5	.724	1.21	
1/			

1/ Data on number of instars are incomplete.

precisely because of low numbers and their sensitivity to frequent handling which contributed to a high rate of mortality. In soil, larvae took from 79 to 96 days to reach the prepupal stage and the prepupal period was ca. 14 days. No individual that pupated, emerged as an adult in the pupation study; therefore, the length of the pupal stage was not determined.

The preoviposition period of newly emerged adults was 21 days. Adults laid ca. 3.5 eggs/day for extended periods. Adults collected from the field did not live more than 2 months. No figures were secured for laboratory-reared adults.

Eleodes obsoleta: The measurements from 111 eggs ranged from 1.7 to 2.3 by 0.98 to 1.33 mm. These eggs were only exceeded in size by those of E. tricostata. The incubation period was 8 days at 24°C.

The number of instars, average head capsule widths, growth ratios, and the average number of days spent in each stadium are shown in Table 6. There was an average of 9 instars; however, a few larvae pupated after 8 instars while 2 developed 10 stadia before pupating. The average time spent in the larval stage was 151.7 days. The prepupal stage lasted 6.8 days, and the pupal stage lasted 19.9 days.

The preoviposition period was not determined. Adults laid ca. 2-4 eggs/day for 1.5 months. The adult life in the laboratory was only 2 months.

Table 6.--Average head capsule measurements, growth rates, and growth ratios of E. obsoleta.

Instar	Av head capsule width (mm)	Growth ratio	Av duration (days)
1	0.58		1.3
2	.69	1.19	14.0
3	.80	1.16	17.2
4	.96	1.20	11.6
5	1.16	1.21	16.0
6	1.38	1.19	19.8
7	1.64	1.19	23.3
8	2.00	1.22	20.2
9	2.21	1.11	28.3

Embaphion muricatum: The eggs were oval and the surfaces were smooth and milky white when laid. They turned to a yellowish color just prior to hatch. The measurements from 104 eggs ranged from 1.20 to 1.35 by 0.65 to 0.78 mm. When eggs were incubated under various temperatures, the optimum temperature was determined as 24°C (Table 7). Eggs held at 29°C had a shorter incubation time but there was a reduction in the number that hatched. Those eggs held at 13 and 18°C failed to hatch and were attacked by fungi.

Table 7.--Effect of various temperatures on egg hatch of *Embaphion muricatum.*

Temperature (°C)	No. eggs	% of eggs hatched	Incubation time (days)
13	60	0	-
18	60	0	-
24	60	98.3	7 - 9
29	60	81.0	4 - 8

The number of instars, the average head capsule measurements, and the growth ratios are shown in Table 8. One larva pupated after the 11th stadium, and a few pupated after the 13th, 15th, and 16th stadia. However, most of the larvae pupated after the 14th stadium. The growth ratio was consistent until after the 11th stadium; however, the growth ratio decreased with each successive molt thereafter.

The average length of the larval stage reared in soil was 76 days and ranged from 70 to 83 days. During the last instar, larvae became lethargic, ceased feeding, and entered the prepupal stage which lasted ca. 4 days. The pupal stage lasted from 10 to 16 days and averaged 13.4 days; this was considerably shorter than the figures reported by Wade and Boving (1921).

Table 8.--Average head capsule width and growth ratio (Dyar's Law) of each larval instar of Embaphion muricatum.

Instar	Av head capsule width (mm)	Growth ratio (Dyar's Law)
1	0.40	
2	.50	1.25
3	.60	1.20
4	.70	1.17
5	.80	1.14
6	.92	1.05
7	1.04	1.13
8	1.18	1.13
9	1.34	1.14
10	1.51	1.13
11	1.71	1.13
12	1.86	1.09
13	1.98	1.06
14	2.10	1.06
15	2.15	1.02
16	2.17	1.01

The preoviposition period was 10-14 days. The rate of oviposition is shown in Table 9. The average rate was 5.36 eggs/female per day over a period of 29.7 days. It appeared that adult females were capable of ovipositing ca. 159 eggs during a 4-week period. The life expectancy of adults in the laboratory was from 3 to 4 months.

Table 9.--Rate of oviposition of *Embaphion muricatum* in the laboratory.

Replicate no.	No. females	Total days	Total no. eggs	Eggs/♀ per day
1	5	10	54	1.08
2	5	43	1184	5.51
3	5	43	703	3.27
4	5	42	868	4.13
5	5	43	964	4.48
6	5	34	1259	7.41
7	5	33	1396	8.46
8	5	26	609	4.68
9	5	20	887	8.87
10	5	3	37	2.47
Av	5	29.7	796.1	5.36

Field Investigations

Materials and Methods

Adults of false wireworms are flightless and exhibit a crepuscular or nocturnal activity pattern. They are only found with difficulty during the day because they seek shelter under objects or in cracks in the soil. Therefore, to sample the populations adequately, some method was necessary to trap individuals when they were active. Pitfall traps worked nicely for this because beetles readily entered but could not escape. Two types of traps were used in this study. Pitfall traps used by Matteson (1966a) to survey populations and to collect beetles for inclusion in laboratory colonies consisted of 1-pt mason jars each with a screened hole in the bottom to allow the water to drain out. The tops were fitted with metal funnels and secured with the metal screw ring. These traps were buried flush with the soil, and an area 6 in. in diam around each trap was cleared of debris and plant material.

Another type of pitfall trap, a trough trap, was designed to capture these insects more efficiently. The trap was constructed from galvanized metal and measured ca. 36X4X2 in. The 2-in. opening on top had a 1-in. lip on each side which was bent downward at a 45° angle. This allowed the insects to tumble in but prevented them from crawling out. Also, the overhanging lips provided shade at the bottom which helped reduce mortality from direct sunlight. These traps were also buried flush with the soil surface, and all vegetation and obstacles were cleared from a 6-in. band around each trap. Greenslade (1964) reported that when vegetation was removed from around pitfall traps, more insects were collected. The procedure also reduced the amount of trash that would have fallen into the traps.

The jar traps were used in 1964, 1965, and 1966, and the trough traps were used in 1967 and 1968 in an attempt to capture a larger number of beetles.

Fields selected as trapping sites were located within general areas of the state having large acreages of wheat and desirable soil types. Fields that were near paved highways were chosen to facilitate long distance surveying in as short a time as possible. The soil-type areas were located by use of soil maps (Westin and Buntley 1962a, 1962b).

Trapping periods and field locations varied from year to year because of cropping sequences. Most wheat farmers in the semi-arid portions of the state practiced summer fallowing on alternate years between wheat crops. In other parts of the state, most small grain fields were rotated with other crops. Harvesting and weed control practices resulted in premature termination of trapping at some sites. For example, wheat was normally harvested during July in southwestern South Dakota. Combines or grain trucks usually managed to drive over traps that were still present. During August, these fields were disked to control wild buckwheat and other late-summer weeds; any previously undamaged traps were certainly destroyed in this operation. Therefore, it became necessary to remove the traps from fields in the southwestern part of South Dakota in July and to relocate them in fields farther north where late-summer weed control was not as widely practiced.

Many workers have indicated that false wireworms were most numerous on knolls and along edges of grain fields (Wade 1921, McColloch 1922, Wade and St. George 1923, Wakeland 1926). Traps were thus placed in grain fields on high level areas or at the crest of knolls and ca. 20 ft into the field whenever possible. Traps were set in groups of 3, usually 5-10 ft apart, at each location.

The number of field locations as well as the time that traps were present at each location were variable within and among years. Therefore, all data were reduced to the number of beetles caught per 10 locations/day regardless of the actual number of locations involved. The corrected data removed the bias involving unequal numbers of locations and the extremes of daily weather effects.

The location of trapping sites for each year from 1964 to 1968, along with a brief description of each site and the dates the traps were in operation, is shown in Addendum I. Traps were visited at intervals of from 6 to 14 days. Beetles were usually found alive, but if they had died, the elytra were always present so that accurate identification and counts could be made. Careful records of all beetles captured at each location were made using standardized forms. Live beetles were placed in compartmentalized screened wooden boxes and returned to the laboratory for additional studies.

Results

Table 10 shows the seasonal appearance of each species in pitfall traps from April 16 to October 15 for 1964 through 1968. The season was divided into ca. 15-day intervals. When beetles were removed from the traps, the information was recorded for that date. However, the beetles were probably not caught on that date but on any of the days the traps were in operation since they were last emptied. The periods between check dates frequently overlapped the 15-day intervals set up in the table, and the time periods between checks were unequal within seasons as well as among years. Therefore, it was necessary to reduce the collection data to beetles captured per day and only include the portions of the sample that occurred during each respective interval. The data were thus converted to whole numbers and fractions which were difficult to interpret. Therefore, the figures were changed to percentages of beetles caught during each interval throughout the 5-yr period. The variation in daily catches was great, but by averaging the capture data over 5 years, a general picture of seasonal abundance emerged.

The seasonal occurrence of each life stage of each species as determined in this investigation together with observations by other workers is shown in Table 11. Cited data are followed by a letter indicating reference citation. These combined statistics give a complete picture of the life cycle of each species and show how the seasonal appearance of each stage varies from species to species.

Table 10.--Seasonal appearance of false wireworm adults in pitfall traps in South Dakota. 1964-1968.

	Percentage of beetles found each 15-day period											
	April	May		June		July		Aug.		Sept.		Oct.
	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-31	1-15
Eleodes suturalis	0.4	0.2	2.7	8.3	15.6	20.6	19.6	16.4	6.9	4.1	3.0	2.3
E. opaca	0	0	0	0.7	4.9	10.6	16.0	18.7	25.8	17.8	5.4	0
E. hispilabris	0	0	0.8	4.6	4.1	5.0	7.7	12.5	21.8	20.7	18.3	4.6
E. tricostata	0	0	.9	3.7	4.6	7.0	23.3	25.2	19.2	12.6	3.3	0.2
E. extricata	0	0	0	0	0	0	2.1	22.9	34.1	14.6	17.3	8.9
E. obsoleta	0	0	.4	.2	0.1	0.5	4.2	13.8	26.0	27.2	24.3	3.4
Embaphion muricatum	.1	1.2	4.1	7.7	13.1	29.3	19.7	9.1	6.4	3.7	4.5	1.2

Table 11.--Seasonal occurrence of eggs, larvae, pupae, and adults of false wireworms found in South Dakota.

Species	Egg	Larva	Pupa	Adult	Overwintering stage
Eleodes suturalis	Spring-late summer[i]	All seasons[i]	Spring-late summer[i] Spring and early summer[c]	All seasons[i] June-Sept.[f]	Adult[i] Larva[i] 10th instar[c] Mature larva[g]
E. opaca	July-Oct.[e] July-Oct.[g]	Aug.-May[g]	April and May June[e] May-July[g]	May-Oct.[e] June-Sept.[g]	Larva Mature larva[e,g]
E. hispilabris	Spring[j] May and June[k] May-Nov.[b]	Aug.-June[k]	July[k]	May-Oct. June-July[f] July-Aug.[j] Aug.-June[k]	Larva[b,k] Adult[b,k]
E. tricostata	July-Oct.[d]	July-June[d]	May-July[d]	May-Oct. June-Nov.[d]	Adult[d,e] Next to last instar[e]
E. extricata	Fall	June-May[k]	June-July[k]	July[k] July-Oct.	Adult and larva[j]
E. obsoleta	Aug.-Oct. Aug.-May[a]	May[a]	June[a]	May-Oct. Aug.-Oct.[a]	Larva Egg[a]
Embaphion muricatum	May-June[h]	June-Apr.[h]	May[h]	June-May[h]	Adult and mature larva[h]

a/ Blumberg (1961)
b/ Haverfield (1965)
c/ Matteson (1966a, 1966b)
d/ McColloch (1918)
e/ McColloch (1919)
f/ McColloch (1922)
g/ Swenk (1923)
h/ Wade and Boving (1921)
i/ Wade and St.George (1923)
j/ Wakeland (1922)
k/ Wakeland (1926)

Eleodes suturalis: Adults appeared during each 15-day interval throughout the sample periods. Those appearing in late April probably overwintered as adults. Newly emerged adults, as evidenced by a brighter, deep glossy appearance, began appearing in the traps near the end of May. Since the preoviposition period was found to be ca. 28 days, the 1st eggs from the new generation adults probably were deposited near the end of June, and oviposition probably continued until September. Larvae from the eggs laid by the overwintered adults and the earliest eggs deposited by the new generation adults probably reached the 10th instar by September and normally would not pose a threat to fall-seeded grains because feeding by larvae in that stage is greatly reduced (Matteson 1966a, 1966b). Larvae in the 4th-6th instars feed actively and pose the greatest threat to fall-seeded grains. These probably hatched from eggs deposited during August. The highest number of adults were caught during July, and the oviposition rate of these adults would probably be highest during August and early September. The larvae that hatch early in the summer do not pupate because of an obligatory diapause (Matteson 1966a, 1966b). Those that hatch later probably do not reach the 10th instar until fall, but because of the diapause phenomenon, almost all larvae would be in the same stage of growth when cold temperatures occurred. All adults would not be expected to emerge simultaneously in the spring because of variations in the speed of development among individuals and variations in the microenvironment. For instance, a north-facing slope would be much cooler and more moist than a south-facing slope. The difference in temperatures would be enough to cause a difference of several days or weeks in development. This is probably of benefit to the species because a single catastrophe (e.g. late freeze, fire, or rain storm) would not seriously deplete the population. In fact, the occurrence of such catastrophes probably select against short-term emergence.

The peak population of adults occurred during July (the month of harvest). There are usually numerous seeds scattered over the ground during the harvesting operation, and these serve as food for both adults and newly hatched larvae. Some kernels persist without germinating for several weeks after harvest and continue to serve as food for these insects. The seasonal biology of this species is synchronized with the planting dates in such a way that these insects pose a serious threat to fall-seeded grains. However, they would probably not threaten spring-seeded grains because the larvae present in the spring are about to pupate.

Eleodes opaca: The peak adult emergence occurred during late August. The oviposition peak probably occurred in September, because the preoviposition period is 6-9 days. Early larval growth is rapid which would allow partly grown larvae to be present during the fall seeding of winter grains. From laboratory investigations of the biology, there was a period of very slow growth at ca. the 5th instar. The timing of this would coincide with the onset of cold temperatures. This phenomenon was apparently not an obligatory diapause because the species could be reared successfully at constant warm temperatures.

However, because this stage and the cold temperatures occur simultaneously, a diapause would not be necessary to synchronize the development of the population. Further evidence is shown by the fact that no adults were found before June 1 and only a few were present before July 1. This fact would also indicate that additional larval growth occurs in the spring. Indeed, larvae have been observed feeding in grain fields in April and May. Because larval feeding occurs in both the fall and the following spring, this species poses a threat to both fall- and spring-seeded grains.

Eleodes hispilabris: No adults were collected prior to May 15. However, the number of beetles captured each year was always small. The number of adults found in the traps increased only slightly throughout the summer but much larger numbers were trapped in August and peak numbers occurred in late August and early September. The preoviposition period of at least 3-4 weeks (which was true of beetles collected in South Dakota) and the incubation period of 10-12 days would put the appearance of larvae at ca. October. The overwintering stages would thus be very young larvae and adults. Laboratory studies revealed that this species appeared to have a facultative diapause in the later instars that was successfully broken by ca. 60 days of near freezing temperatures. These larvae would probably pupate during the following spring. This would explain the appearance of adults in late summer but would not explain the life cycle of those young larvae that overwinter. These larvae would not pupate until they have gone through an additional winter as mature larvae.

This would mean that some individuals would live as much as 1.5 yr in the larval stage.

If adults overwinter and do not emerge from hibernation until very late spring as observed by Wakeland (1926), it would explain the almost total absence of adults in April and early May. Then, larvae from eggs deposited in June and July would reach maturity by late fall and would overwinter in that stage. Pupation would take place the following spring and adults would emerge beginning in August. These adults would then overwinter. Therefore, mature larvae and adults of 2 different generations would overwinter simultaneously. This appears to be the most logical explanation.

Larvae approaching maturity in September would probably feed until they reached the stadium in which overwintering occurred. Therefore, larvae capable of feeding on grain sowed in September would be present and, if populations were high enough, economic damage would occur. However, this insect would not appear to be a threat to crops planted in the spring.

Eleodes tricostata: Adults were 1st captured in late May. However, the population levels remained low until late July and August. The sudden population increase was undoubtedly due to young adults emerging from pupal cavities. The population remained relatively high until late September when it declined quite drastically. The life cycle of this species resembled the life cycle of E. opaca except that the larvae almost reached maturity in the fall and probably did not have a lengthy feeding period during the following spring.

Because this species was found to be confined to native grassland in the larval stage (McColloch 1918), and adults were only found in wheat fields in low numbers in South Dakota, it probably would never be a threat to wheat crops in South Dakota.

Eleodes extricata: No adults were captured until late July. The peak adult population occurred in late August and rapidly declined thereafter. Adults did not appear to overwinter as indicated by these trap catches. Eggs were deposited during August and September. The larvae probably overwintered when partly grown and resumed growth and feeding the following spring. Since feeding occurs during both the fall and spring, this species poses a threat to fall and spring grains.

Eleodes obsoleta: Adults were 1st found in late May in very low numbers, and no substantial increase in numbers occurred until August. The population reached a peak in late August and remained high throughout September, then dropped very drastically in October. The appearance of adults in May indicated that a very few were able to overwinter. Adults collected from the field in August immediately began to lay eggs when brought to the laboratory. These eggs hatched in ca. 8 days and the young larvae began feeding. If this species overwinters in the egg stage as suggested by Blumberg, the eggs deposited throughout August and September would require a diapause to prevent hatching prior to winter. This diapause would be broken after exposure to cold temperatures much like the larval diapause of E. suturalis. Obviously, this species does not have an egg diapause in South Dakota. Overwintering occurred in the partly grown larval stage at no particular instar. The pupal stage probably occurred during July. The larval period lasted for ca. 152 days in the laboratory. During the life cycle in the field, part of this active feeding stage was present in the fall and the remainder occurred in the spring. Thus, this species has the capability of being destructive both in the spring and in the fall.

Embaphion muricatum: Adults of this species were captured during each 15-day interval that traps were operated. Relatively low numbers of adults were trapped except during late June and throughout July. The life expectancy of the adult was determined in the laboratory as being 3-4 months, but the appearance of beetles in the field early in the spring indicates that some adults apparently overwinter; this extends the life expectancy considerably. The oviposition period of several weeks and the absence of a diapause mechanism in the larval stage allow larvae of several stadia to overwinter. Pupation probably occurred in May. Larvae were present in both fall and spring, but because larval and adult stages occur over such a long period of time, the impact of the population would not be as great as if the actively feeding stages were concentrated into short time periods. This species could be economically important if the population was high, but a higher overall population would have to exist for this species to be as economically important as such other species as Eleodes suturalis and E. opaca.

CHAPTER II

DISTRIBUTION OF FALSE WIREWORMS

The distribution of an insect species is an integral part of its ecology. It is a reflection of the environmental conditions necessary for its survival provided that the distribution is not limited by the range of its hosts. This is especially true of species like false wireworms that have a low rate of mobility. The geographic distribution should allow insights into the climatic parameters involving its survival. For instance, the northern boundary of a species distribution usually relates to its tolerance of low temperatures. If its distribution is related to rainfall, it may be affected by related conditions such as soil moisture levels, relative humidity, etc., and its distribution would be limited at some point along a rainfall gradient. On a smaller scale, the distribution in relation to pedographic patterns is correlated more closely to species inhabiting the soil during some stage of their life cycle than to those not inhabiting the soil. Soil type differences are related to porosity, structure, water holding capacity, or to some chemicals associated with a particular soil.

On a still smaller scale, distribution within a small area ranging from a few square miles to a few square inches probably is more closely related to the microenvironmental parameters of an insect's life cycle. Much of this type of distribution is related to topography which in turn influences temperature, soil moisture, and vegetation. A species thought to be adapted to a wide range of environmental factors may, in fact, be found restricted to micro-environments that have relatively narrow parameters.

The understanding of topographic, pedographic, and geographic distributions of a species allows insights into the relationships existing between the organism and its environment. This understanding is necessary for development of precise control measures based upon sound ecological principles.

Localized Distribution and Movement of False Wireworms

In South Dakota, most infestations of false wireworms are moderate and typically occur in localized areas rather than uniformly throughout a field. Such localization probably reflects the ovipositional sites used by the adults because the range of movement of larvae underground is limited. Wade and St. George (1923) stated that infestations usually occurred around straw stacks, grain shocks, and field edges where the adults tended to congregate, but machine combining of the standing grain (a modern method of harvesting) now causes the straw to be evenly distributed over the field. In the absence of such accumulations of straw and chaff, the adult beetles probably respond to preferred natural environments within the fields.

Most damage by false wireworms observed in wheat fields in South Dakota in recent years occurred on knolls and slopes and along the edges of fields. Because these areas might be the preferred oviposition sites or might merely reflect maximum larval survival, a study was made to determine the localized distribution of adult false wireworms and to determine whether the sites of concentrations of the adults were correlated with observed damage. In addition, because false wireworms are flightless, determinations of their range, rate, and direction of movement and their longevity in nature was needed to understand the factors determining distribution.

Materials and Methods

The study was conducted in Haakon Co., S. Dak., in a field of winter wheat that had a moderately high population of false wireworms. The field, ca. 80 acres, contained several typical topographical features such as extensive level areas broken by knolls and slopes, a shallow draw through the middle of the field that provided opposing north- and south-facing slopes, and native grass bordering on 3 sides with alfalfa on the 4th (Fig. 2).

Five species of false wireworms were found in the field in sufficient numbers to be included in the study. They were *Eleodes suturalis*, *E. opaca*, *E. tricostata*, *E. obsoleta*, and *Embaphion muricatum*. Adults of these species are not able to fly because their elytra are fused. Also, they are nocturnal and spend the daylight hours under rocks and trash and in cracks in the soil. Therefore, I used the trough type pitfall traps to determine their presence in particular areas. The traps were numbered and trap locations were platted on a map of the field.

Because the field was located 260 miles from the laboratory, the traps could be checked only weekly. However, most *Eleodes* beetles

Fig. 2. A view of the wheat field in which the localized distribution and movement study was conducted (Haakon Co., S.D.).

seemed to be hardy since they remained alive in the traps for over a week without food or water. These beetles also possess a defensive secretion that protects them from being eaten by predators (Blum and Crain 1961, Roth 1945, Wade 1921). However, if death occurred, the elytra remained in the traps so that identifications and counts could be made.

Movement of the Beetles.--To determine the range, rate and direction of movement, and longevity of the beetles, a mark-and-release technique was used in a specially selected, extensive level area of the field. Pitfall traps were arranged in 3 concentric circles at 90° angles around a release point. The inner circle was 120 ft in diam and consisted of 8 equally spaced traps, the 2nd circle was 240 ft in diam and had 12 equally spaced traps, and the outside circle was 360 ft in diam with 16 equally spaced traps.

The beetles used in the study were obtained by emptying the traps each week and noting the number and location of each species. A different color of Vogart Embroider Paint® was applied to the healthy, active beetles in each week's collection. (This nontoxic paint lasted several weeks even when the beetles burrowed beneath soil and other types of cover.) The marked beetles were then released at the center point of the circles where the soil in a 2-ft^2 area was loosened to provide immediate shelter. Thus, the dispersal from this point occurred more naturally than if the beetles were scattered on bare soil.

Distribution of Beetles.--To study the distribution of a natural population of false wireworm beetles in relation to the field edge, pitfall traps were placed 10 ft from the field edge in the bordering grassland, and 10, 40, 70, and 100 ft into the field. Since the traps were set at a 45° angle to the rows, beetles traveling with the rows had as much chance of being caught as those traveling across rows. The 5 trap-positions were replicated 4 times. The traps were checked weekly, but the data were grouped into 3 trapping periods that appeared to represent clearcut ecologically different situations. Thus the 1st period (early summer) was from June 18 to July 2 when rainfall was moderate (5.89 in.), temperatures were cool (65.3°F), and the vegetation was green and growing. The 2nd period (midsummer) was from July 9 to July 30 and was characterized by warmer temperatures (74.8°F), less rain (0.84 in.), ripening grain, and much more light at ground level. The 3rd period (late summer), from Aug. 27 to Sept. 26, was characterized by cooler air temperatures (63.2°F), little rain (0.47 in.), and ground cover that consisted of grain stubble.

Distribution and Topography.--The effect of topography on distributions of the beetles was evaluated on opposing north- and south-facing slopes that had environments like those reported by Jackson (1966), Parker (1952), Potzger (1939), and Shreve (1924). In essence, south-facing slopes are more perpendicular to the angle of the sun's rays than are north-facing slopes, hence they provide a warmer, drier environment. On the south-facing slopes in this test, the vegetation appeared shorter and less luxuriant than on the opposing slope. Also, there appeared to be a difference in the lushness of the vegetation from top to bottom on both slopes: the bottoms were more moist and humid, and the vegetation reflected this condition by being more dense and rank in growth; the tops were drier, and the plant growth was much shorter and less dense. Pitfall traps were therefore set at the top, middle, and bottom of each slope in 4 replicates spaced horizontally 50 ft apart. The traps were examined weekly.

Results

Movement of Beetles.--The number of beetles of each species marked and released each week throughout the summer is given in Table 12. *Eleodes suturalis* and *E. opaca* were collected, marked, and released every week of the study. *Eleodes tricostata* was collected in adequate numbers only during the latter part of the summer; *E. obsoleta* and *Embaphion muricatum* were found in low numbers throughout the study. Many more *Eleodes opaca* were marked and released than any other species.

Table 12.--Summary of beetles marked and released throughout the summer in a wheat field, Haakon Co., S. Dak. 1968.

	No. beetles marked and released										
	June		July					Aug.		Sept.	
Species	18	27	2	11	19	25	30	21	27	3	Total
Eleodes opaca	12	50	217	59	62	57	115	117	526	200	1415
E. suturalis	7	3	7	17	11	23	50	23	76	52	269
E. tricostata	2	0	1	3	8	1	3	0	41	43	102
E. obsoleta	0	0	0	0	0	0	2	0	8	20	30
Embaphion muricatum	0	3	2	1	1	2	1	2	5	0	17

The rate of recovery and the movement of marked and released beetles are shown in Table 13. Marked insects of all species were recaptured. The 36 traps comprised 4.8% of the circumference of the 3 circles. Thus, if the marked beetles moved away from the center in straight lines and in random directions with no doubling back into the circles, we would expect ca. a 4.8% recovery, provided there was no mortality. The recovery rate was in fact 5.1%, close to the expected rate. However, it was known that some mortality occurred because a few dead beetles were recovered at the release point. Also, random movement of the beetles probably meant that they entered and left 1 or all of the circles several times, which would increase the probability that they would be recaptured.

Table 13.--Rate of recovery and movement of false wireworm beetles marked and released in a wheat field, Haakon Co., S. Dak. 1968.

Species	No. beetles recovered	% recovery	Days to capture after release		Distance (ft) from release point	
			Max	Av	Max	Av
Eleodes opaca	71	5.0	63	12.2	1545	180
E. suturalis	14	5.2	58	16.6	315	151
E. tricostata	13	12.7	23	7.3	180	92
E. obsoleta	4	18.2	23	10.8	1090	469
Embaphion muricatum	3	17.6	22	16.7	351	197

In addition, 12 marked beetles (6 E. opaca, 3 E. obsoleta, 1 E. suturalis, 1 E. tricostata, and 1 Embaphion muricatum) were recovered from traps outside the experimental area. Two were over 1500 ft and 1 was over 1000 ft from the point of release. However, these 3 beetles were all on the far side of a shallow draw, indicating that this type of area does not act as a barrier to movement. The times between release and recapture were 63, 13, and 7 days, respectively.

The longest periods between release and recapture were 63 days for Eleodes opaca and 58 days for E. suturalis. Although adult E. opaca normally have only a short life in the laboratory, they may live longer in nature. Other species such as E. suturalis live as long as 1 year in the laboratory (Matteson 1966).

The average distance traveled before recapture exceeded 100 ft for all species except E. tricostata. The average distance traveled by E. obsoleta was 469 ft from the release site, and the average time of recapture for this species was one of the shortest of those studied. These facts, together with the high rate of recapture of this species, indicate that E. obsoleta is probably more active than some other species.

I divided the capture area into 4 quadrants of a circle (NE, SE, SW, and NW) to determine whether any of the species moved in a particular direction. Then, because each trap was numbered and platted on a map of the field, I could determine the general direction of movement of each beetle that was recaptured. However, only 3 of the 5 species involved were caught frequently enough that I could analyze their movement by X^2 test for a 1:1:1:1 ratio. The results are shown in Table 14. Only E. suturalis tended to show movement in a specific direction, apparently not toward the SE; however, the total number of beetles retrapped was small. For the other 2 species, direction and movement were random, an indication of a general dispersion from the release site.

Table 14.--Direction of movement of marked and released beetles recaptured in traps arranged in concentric circles.

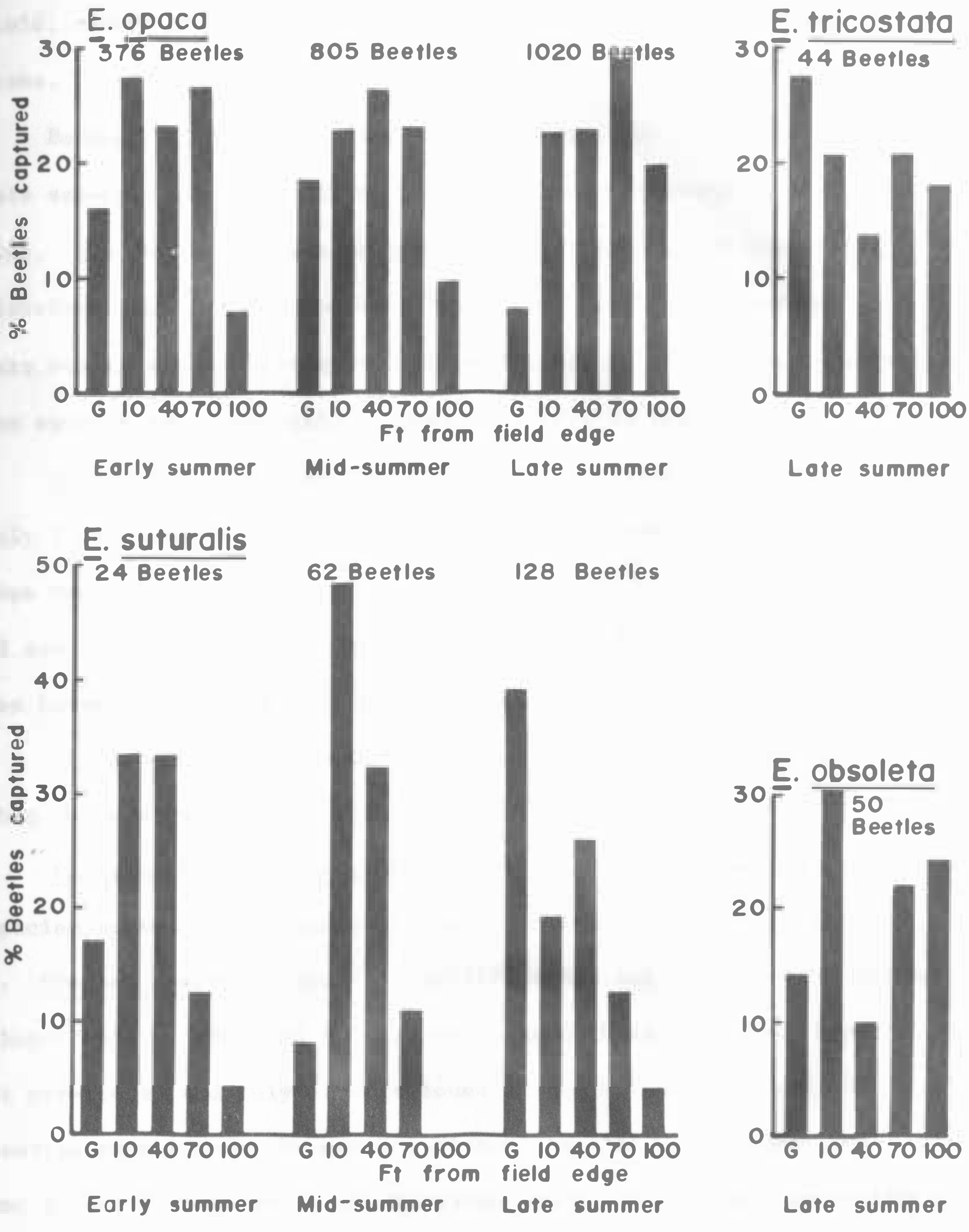
Eleodes species	No. beetles caught in indicated quadrant of circle					
	NE	SE	SW	NW	χ^2	Total 1/
opaca	16	15	10	23	5.94	64NS
suturalis	6	0	3	4	18.74	13**
tricosta	2	4	3	4	2.74	13NS

1/ χ^2 analysis: NS = no significant differences from the expected 1:1:1:1 ratio; ** = highly significant differences from the expected 1:1:1:1 ratio.

Distribution of the Beetles.--The number of beetles of each species trapped and the distribution in relation to the edge of the field during the 3 trapping periods are shown in Fig. 3. Fewer *E. opaca*, the most abundant species, were trapped in the bordering grassland than in the field itself; most of these beetles were captured 10-70 ft from the edge of the field. However, there appeared to be some shift of the population away from the edge of the field during the latter part of the summer. This was the period when the greatest number of *E. opaca* was found and also when the peak oviposition period occurred.

Most of the 214 *E. suturalis* were collected during the late summer. From June 18 to July 30, the largest catches occurred 10-40 ft from the edge of the field; few were caught 100 ft into the field, and few were found in the grassland. Then, from Aug. 27 to

Fig. 3.--Distribution of adult false wireworms from the edge of a wheat field during 3 periods of the summer. G = 10 ft from edge of field in bordering grass.



E. opaca
376 Beetles
805 Beetles
1020 Beetles
% Beetles captured
30
20
10
0
G 10 40 70 100
G 10 40 70 100
G 10 40 70 100
Ft from field edge
Early summer
Mid-summer
Late summer
E. tricostata
44 Beetles
30
20
10
0
G 10 40 70 100
Late summer
E. suturalis
24 Beetles
62 Beetles
128 Beetles
% Beetles captured
50
40
30
20
10
0
G 10 40 70 100
G 10 40 70 100
G 10 40 70 100
Ft from field edge
Early summer
Mid-summer
Late summer
E. obsoleta
50 Beetles
30
20
10
0
G 10 40 70 100
Late summer

Sept. 26, the population appeared to shift toward the edge of the field; almost 40% of the beetles collected were in the bordering grass.

Because E. tricostata was almost absent from the catches until late summer, more than 78% of these beetles were trapped at that time. (So few were taken during the 2 earlier periods that these distributions were not included in Fig. 3.) The distribution in late summer showed little preference for any particular area, although the species was frequently trapped in bordering grass.

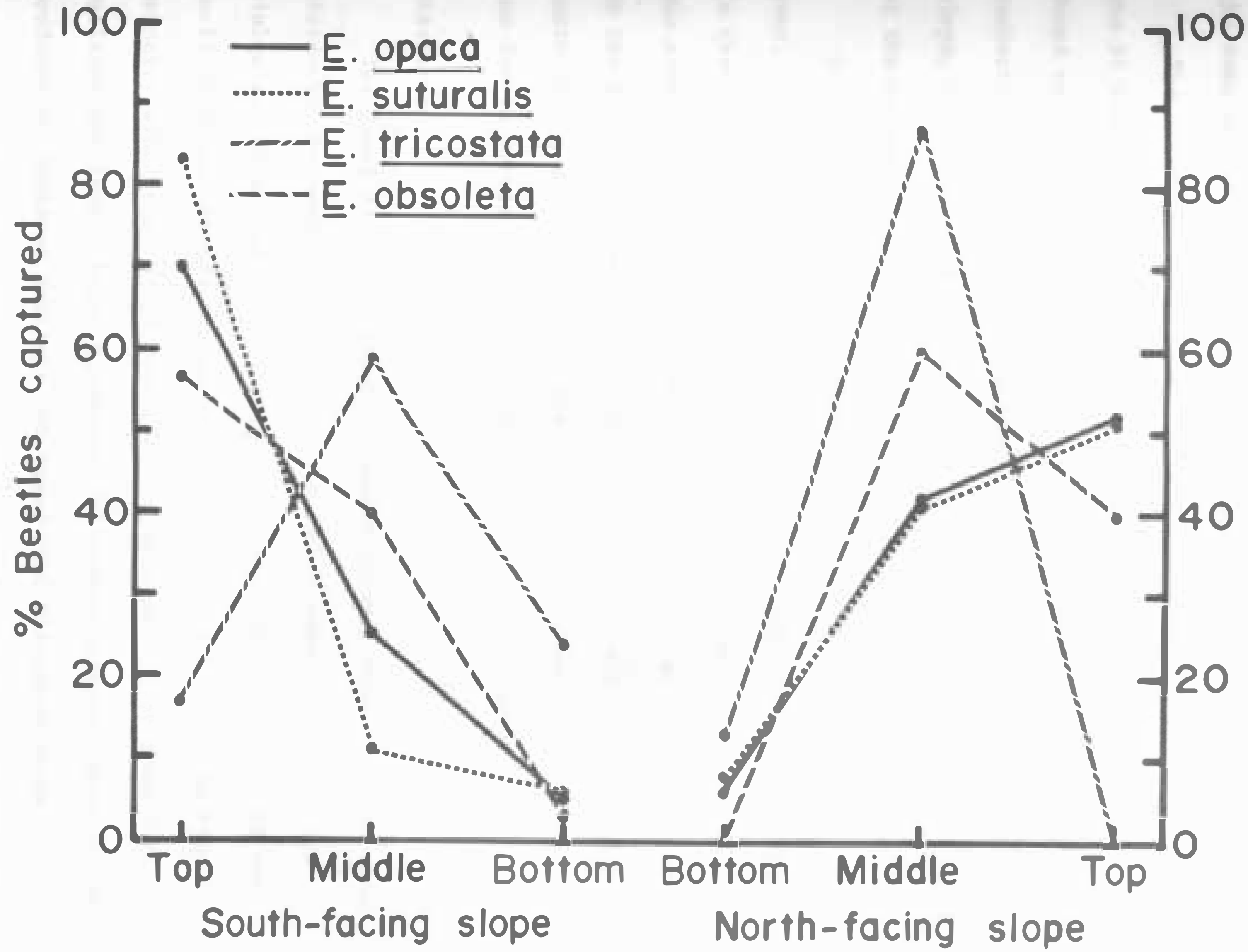
Eleodes obsoleta was found almost exclusively in the late summer; only 1 specimen was found earlier. The distribution from the field edge was fairly uniform: 30% were found 10 ft into the field, and 22 and 24% were found 70 and 100 ft into the field, respectively. The lowest percentage (10%) was collected at the 40-ft distance.

All other species in the study were collected in such low numbers that their distributions were not plotted.

Distribution and Topography.--Distributions of the 4 most abundant species on the north- and south-facing slopes are shown in Fig. 4. Eleodes opaca was found primarily at the top of the south-facing slope: 70% of the 1150 beetles were found there, 25% were found at mid-slope, and only 5% were found at the bottom. Of the 582 beetles captured on the north-facing slope, 51% were at the top, and 43 and 6% were found at mid-slope and at the bottom, respectively.

Also, 83% of the 102 E. suturalis captured on the south-facing slope were found at the top of the slope; 11 and 6% were found at

Fig. 4.—Distribution of adult false wireworms on north- and south-facing slopes in a wheat field.



E. opaca
E. suturalis
E. tricostata
E. obsoleta
% Beetles captured
% Beetles captured
0
20
40
60
80
100
Top
Middle
Bottom
Bottom
Middle
Top
South-facing slope
North-facing slope

mid-slope and at the bottom, respectively. Distribution of the 39 beetles captured on the north-facing slope was almost exactly the same as the distribution of E. opaca.

The distribution of E. tricostata was quite different. Of the 59 beetles captured on the south-facing slope, only 17% were found on top, 59 and 24% were found at mid-slope and at the bottom, respectively. Only 8 beetles were captured on the north-facing slope, but 7 of the 8 were captured at mid-slope, and 1 was captured at the bottom.

Eleodes obsoleta was the least abundant of the 4 species. However, the distribution resembled that of E. opaca and E. suturalis in that 57% of the 35 beetles captured were found at the top of the south-facing slope, and 40 and 3% were found at mid-slope and at the bottom, respectively. Only 5 beetles were captured on the north-facing slope, 2 at the top and 3 at mid-slope; these were too few to permit any conclusions regarding distribution.

Discussion

The fused elytra of false wireworms prevent these beetles from dispersing by means of flight. It is rather hard to imagine the biological advantage of this flightlessness. Certain areas of the world (such as islands and mountain peaks) are subjected to high velocity winds that could sweep air-borne insects away from their isolated habitats. False wireworms, of course, are not necessarily confined to isolated habitats but occur over extensive areas of grassland and desert, and flight would seem to be an advantage in dispersal in their case.

The elytra form a hardened case over the rather fragile abdomen, and Bolwig (1957) has observed that the subelytral cavity so formed by the elytra served to regulate the insect's body temperature. This allowed diurnal beetles to survive high desert temperatures for short periods of time. Other authors (Ahearn and Hadley 1969, Cloudsley-Thompson 1964) have discounted this. Careful experiments in both cases have revealed that the subelytral cavity serves as an effective structure in reducing transpiratory water loss. The elytra are so structured that the spiracles open into this cavity, thus the cavity functions to prevent air currents from moving across the entrance to the spiracles. Cloudsley-Thompson (1964) could find no correlation between the size of the elytral cavity and habitat or time of daily activity. At any rate, it appears that the fused elytra allow tenebrionid beetles to live in extremely dry areas. Thus, the disadvantage of being flightless is far outweighed by the reduction in water loss in these habitats.

Although adult false wireworms are flightless, their lifespan, ability to move over rough terrain, resistance to dry conditions, and safety from predation allow them to travel well beyond the limits of most wheat fields. However, the movements appear to be relatively localized, and large populations several miles away would not seem to pose an immediate threat. Nevertheless, a generalized dispersion does seem to occur during which the beetles move into and out of environments not preferred for concentration. This general reshuffling and the long lifespan of the beetles results in the colonization of most of the preferred sites in an area, and chances that such sites will escape colonization are probably remote except when populations are low. However, the distribution of damage caused by these insects would be patchy at moderate population levels and would only become general when populations were high.

Late summer is the period during which adult populations of all species of the beetle are highest and most oviposition occurs, therefore the distribution of ovipositing females at this time should greatly influence the location of the larvae of the next generation. Also, the distribution of adults of the 2 most abundant species in this study should have been reflected in the damage caused by larvae. In the case of *E. opaca,* distribution did not appear to shift drastically except in late summer, and this shift was away from the edge of the field. However, the population within the field was fairly evenly distributed. In fact, this field had suffered ca. a 60% loss of stand as a result of larval feeding, and the damage appeared to be generally distributed in the flat areas and more pronounced on the knolls (Fig. 2). When larvae were collected and reared for identification, most were found to be *E. opaca.* In the case of adult *E. suturalis,* the population was highest in the bordering grass in late summer, and numbers declined away from the edge of the field. Therefore, damage by this species should occur in border areas. Wade and St. George (1923) did report damage along the edges of fields and attributed it to this species. In our study, we could not attribute damage in that area to *E. suturalis* alone because of the overlapping damage caused by the larger populations of E. opaca.

The populations of E. opaca and E. suturalis on the north- and south-facing slopes changed little throughout the 3 summer periods, and the distributions were almost identical. The distribution of E. obsoleta was similar on the south-facing slope, but a larger percentage of these beetles was found at mid-slope on the north-facing slope. In contrast, E. tricostata was always found in greatest numbers at mid-slope and even more so on the cooler slope than on the warmer, drier south-facing slope.

From the observations just discussed, one would expect E. suturalis to be more prevalent on the tops of knolls and near the edges of fields; E. opaca would probably cause more damage on hilltops and generally throughout level areas of the field; E. tricostata would be found more commonly near the edge of fields and usually on the slopes themselves rather than on the knolls; and E. obsoleta would be found near the tops of hills but would also be scattered evenly throughout the field and even into the bordering grass.

Thus each species of adult false wireworms appeared to have a somewhat different distribution, even though the food habits, life cycles, and larval habits are similar. As a result, they subdivide the habitat among themselves (reducing the competition for food and space and the contact between species) to survive together in the same area.

The study revealed that the only area in the test field that would escape attack from these species would be the bottoms of slopes or low places in fields.

Distribution of False Wireworms in Relation to Soil Type

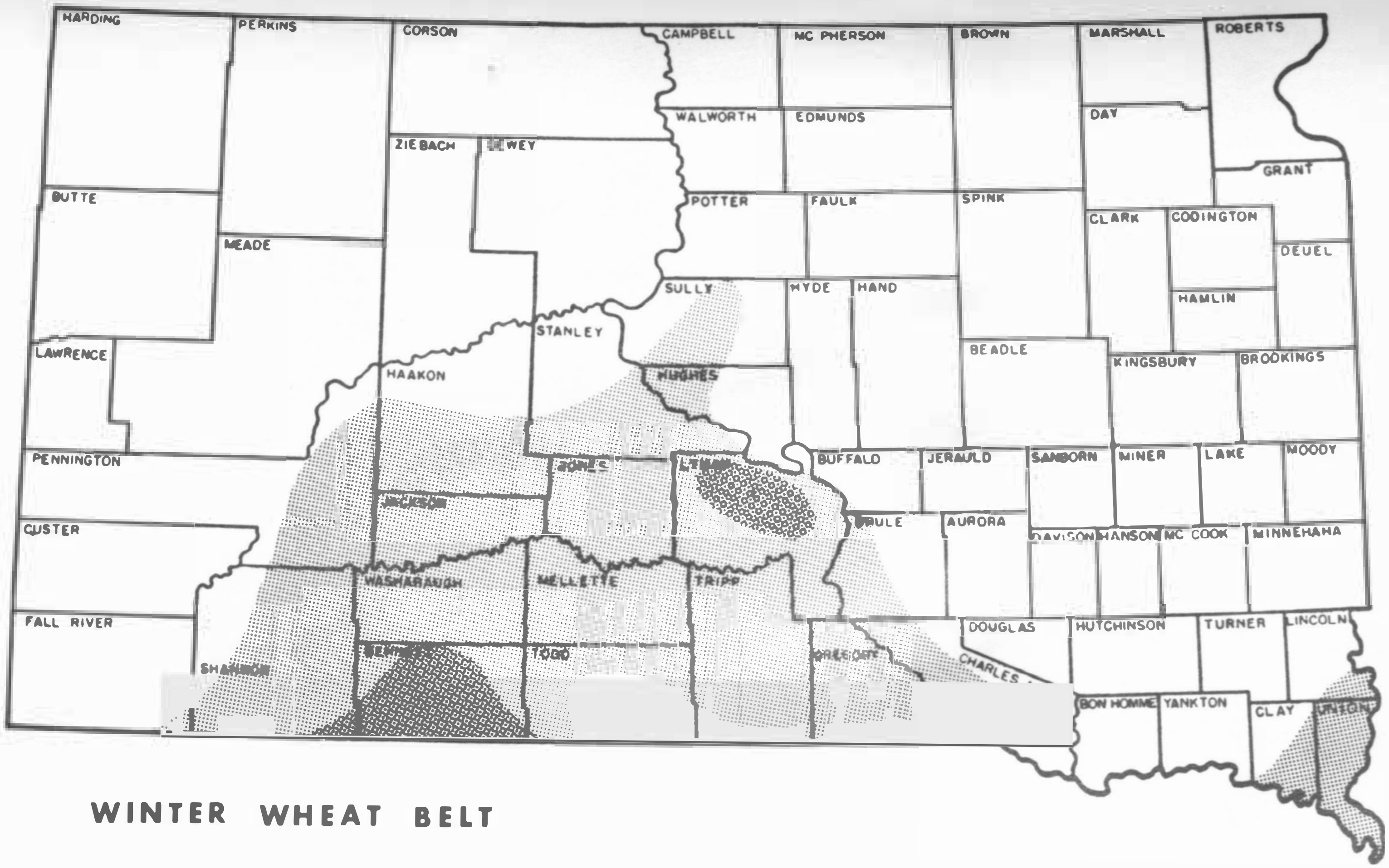
False wireworm beetles have long been characterized as inhabitants of arid regions in sandy or sandy loam soils. "The fact that such soils are much better suited to the multiplication of these insects than those containing a high percentage of clay, has been repeatedly noted by collectors, and the general prevalence in a locality of a hard 'gumbo' or of a clayey surface is not suitable for the best development of these Tenebrionidae" (Wade 1921). McColloch (1922) was only able to collect *E. hispilabris* on sand dunes along the Kansas River. Wade and St. George (1923) observed that the distribution of *E. suturalis* was closely related to the occurrence of light, sandy soils. However, adults were collected in small numbers several miles from sandy locations. Frequent references to the close relationship of false wireworms to sandy soils have resulted in the acceptance of these observations as fact. However, the appearance of damage caused by false wireworms in regions of clay, silt, and loam soils is puzzling. Usually, only the larvae were observed and no identification to species was made. Also, these larvae were frequently misidentified as true wireworms. Therefore, to understand the species composition of false wireworms better in relation to 4 major soil types and to determine the relative abundance of each species in areas of each soil type, this study was initiated.

Materials and Methods

Fields selected for surveying species composition of false wireworms were generally within the major wheat growing areas in South Dakota. Figures 5, 6, and 7 illustrate the 3 major wheat belts in South Dakota. These belts outline the areas of the state where at least 1% of the total acres are devoted to these crops (Westin and Buntley 1962c). Soil type distribution maps (Westin and Buntley 1962a, 1962b) were used to locate areas having clay, silt, loam, and sandy loam soils. Figures 8, 9, and 10 have been adapted from these maps. Some designated soil areas consist of a single soil type, e.g. the dark brown clayey soils of the semiarid grassland; other soil areas are conglomerations of loam soils which range from silt clay loam to loam to sandy loam soils, all in the same general areas. Because this investigation was designed to determine the distribution of each species in relation to soil type, extensive areas of certain types of soil were sought. There was no difficulty in finding extensive areas of clay soils where wheat is commonly grown. However, finding small grain fields in conjunction with other desired soil types was a bit more difficult. Fields consisting of silt soils were not easily located and there usually were fewer such locations selected than sites having the other soil types. In fact, no suitable wheat fields with silt soil were located in 1968.

I became very familiar with those soils that were easily located on the soil maps, and I was able to identify the broad soil types

Fig. 5. Distribution of winter wheat growing areas in South Dakota (Westin and Buntley 1962c).

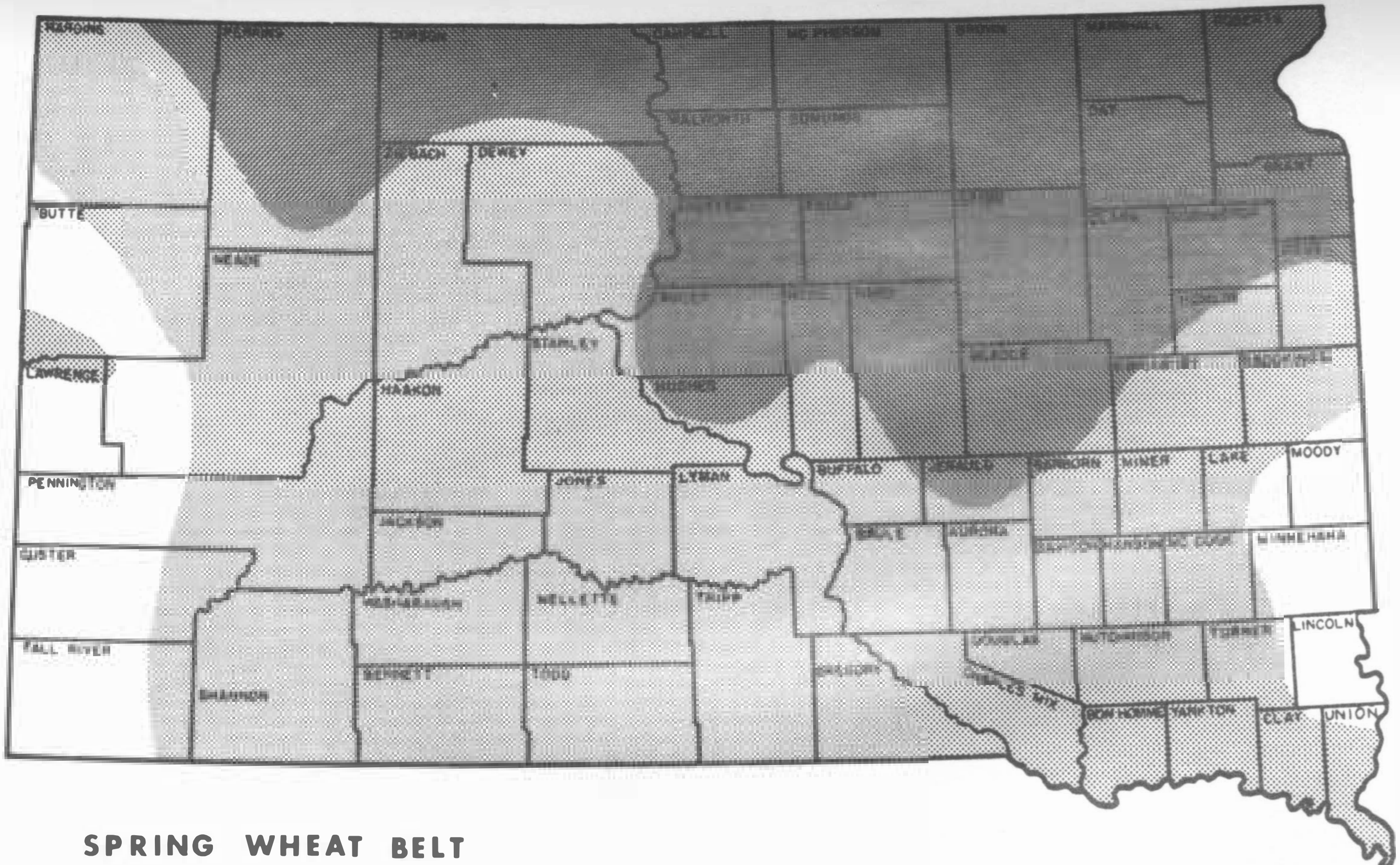


WINTER WHEAT BELT

1% OF TOTAL ACRES

5% OF TOTAL ACRES

Fig. 6. Distribution of spring wheat growing areas in South Dakota (Westin and Buntley 1962c).

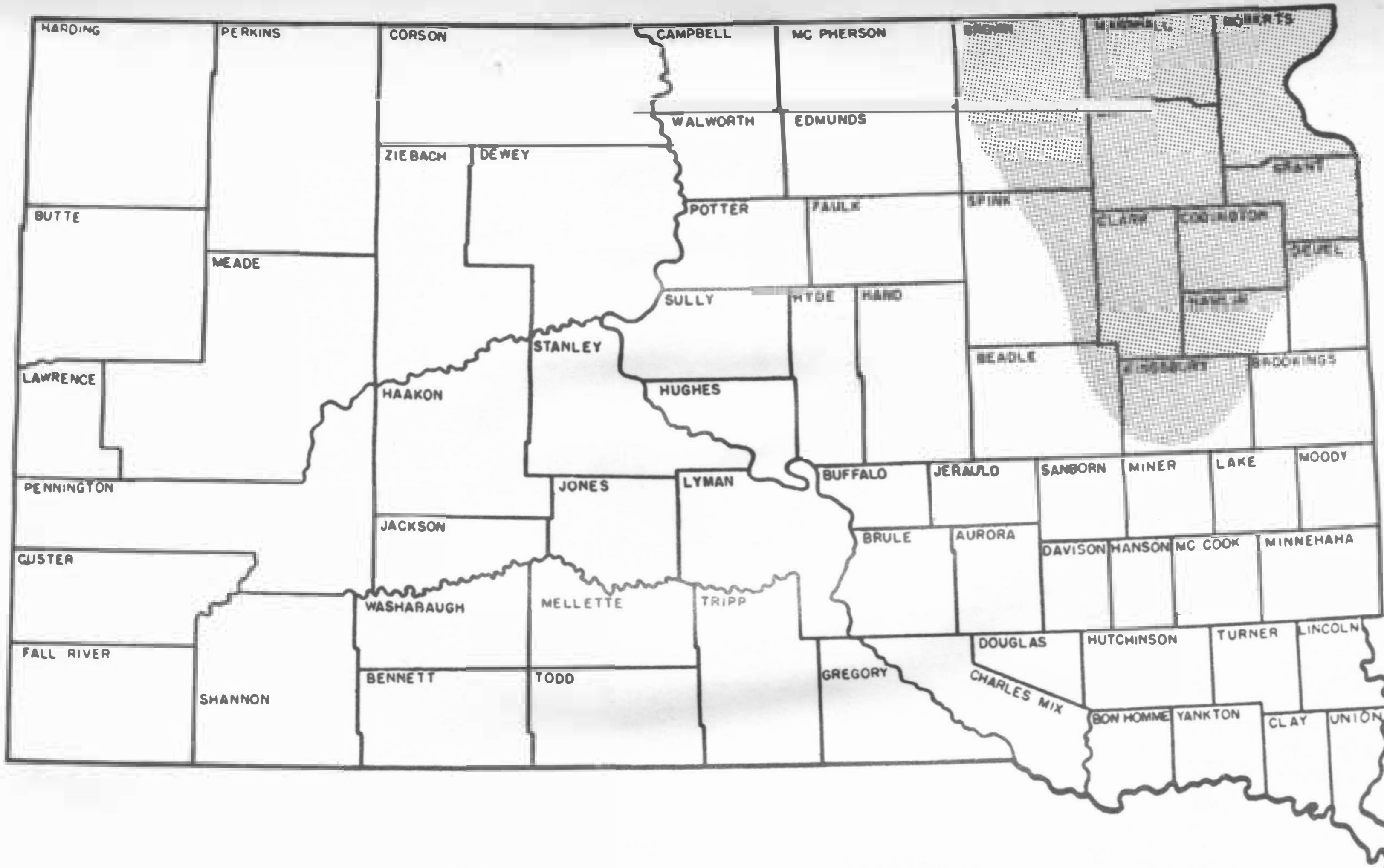


SPRING WHEAT BELT

1% OF TOTAL ACRES

5% OF TOTAL ACRES

Fig. 7. Distribution of durum wheat growing areas in South Dakota (Westin and Buntley 1962c).



DURHAM WHEAT BELT

1% OF TOTAL ACRES

Fig. 8. Distribution of clay soils in South Dakota (Westin and Buntley 1962a, 1962b).

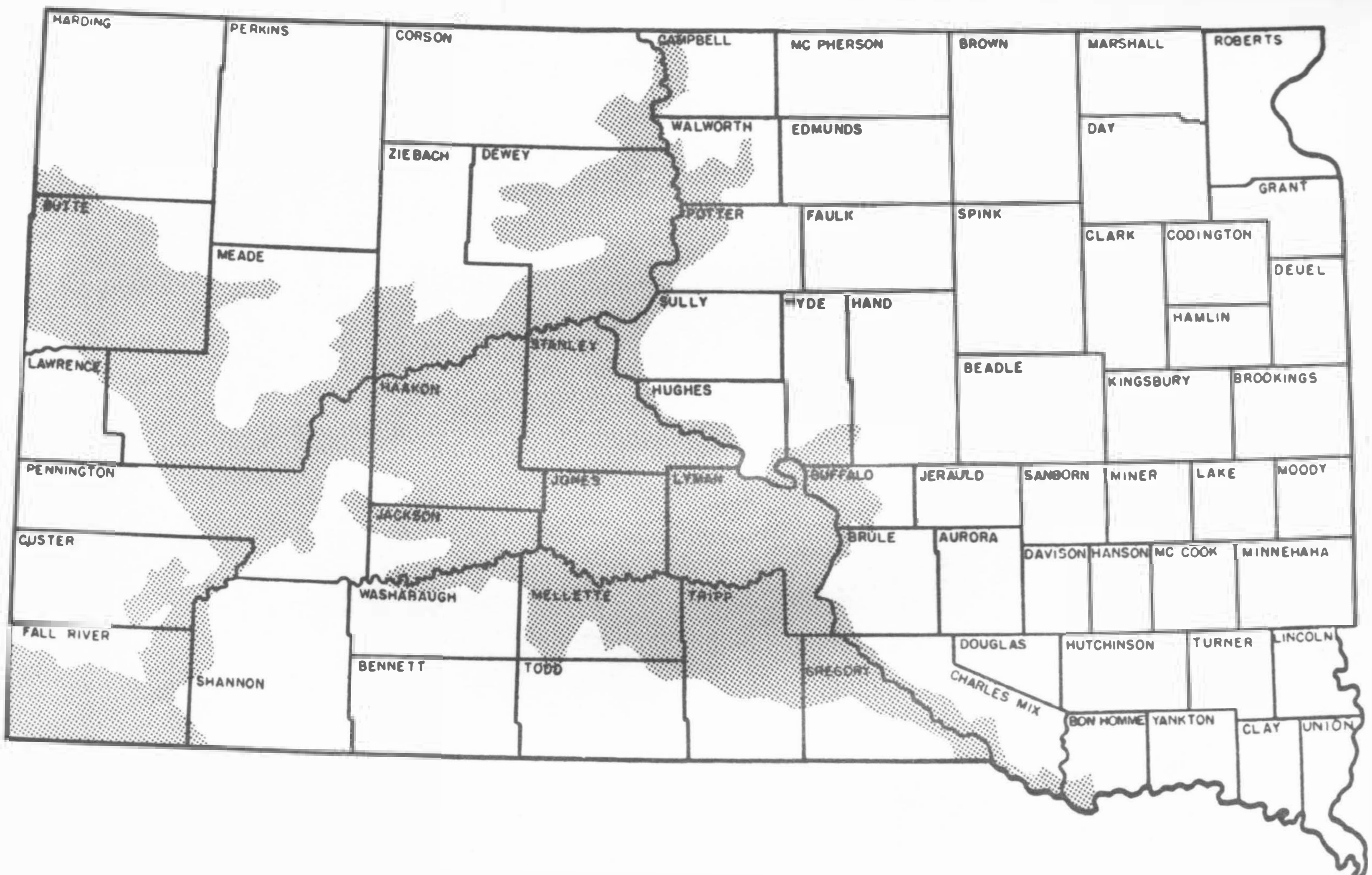

HARDING
PERKINS
CORSON
CAMPBELL
MC PHERSON
BROWN
MARSHALL
ROBERTS
WALWORTH
EDMUNDS
DAY
ZIEBACH
DEWEY
GRANT
BUTTE
POTTER
FAULK
SPINK
CLARK
CODINGTON
MEADE
DEUEL
SULLY
HYDE
HAND
HAMLIN
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Fig. 9. The distribution of clay loam, silty clay loam, silt, loam, and silt loam soils in South Dakota (Westin and Buntley 1962a, 1962b).

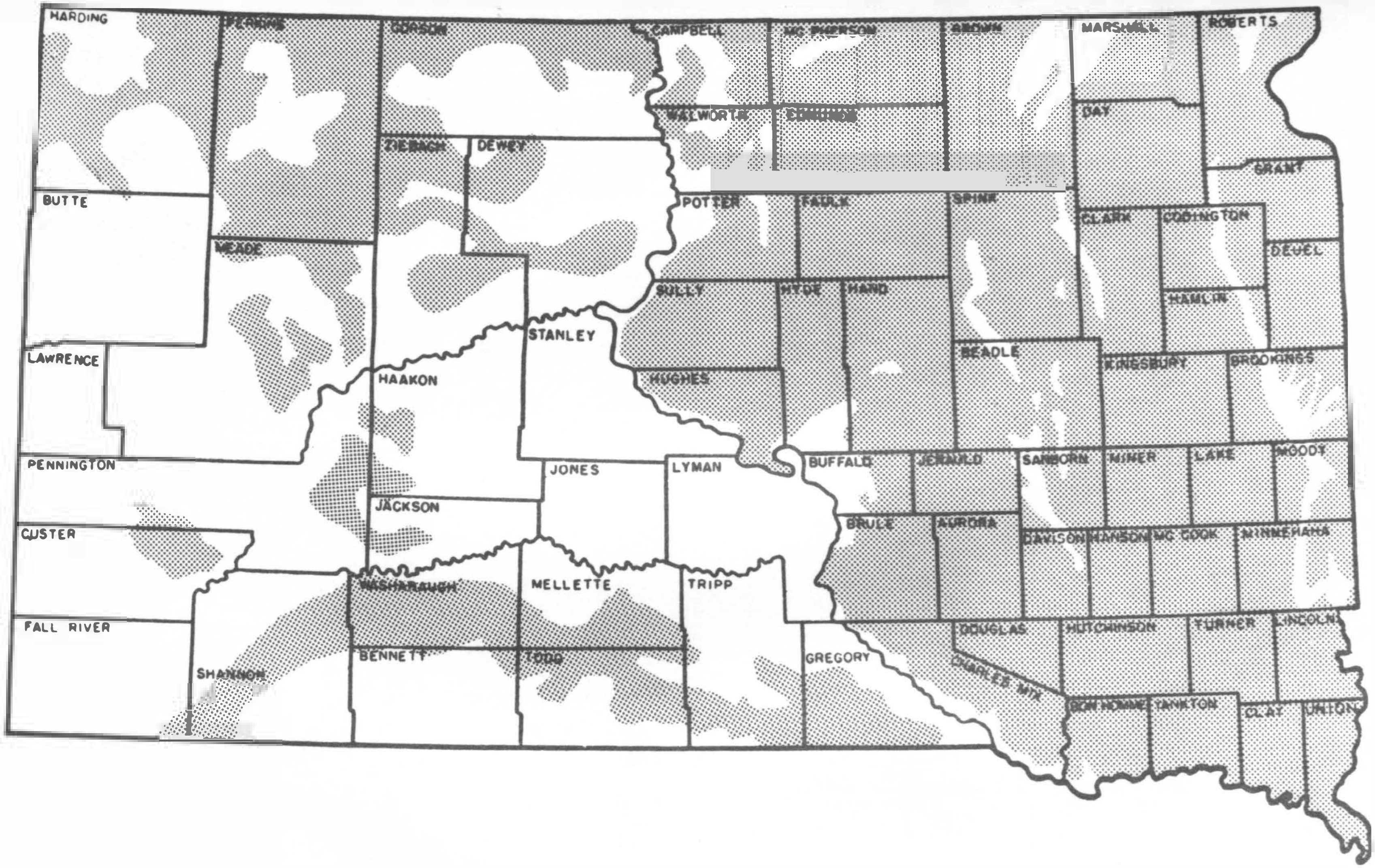
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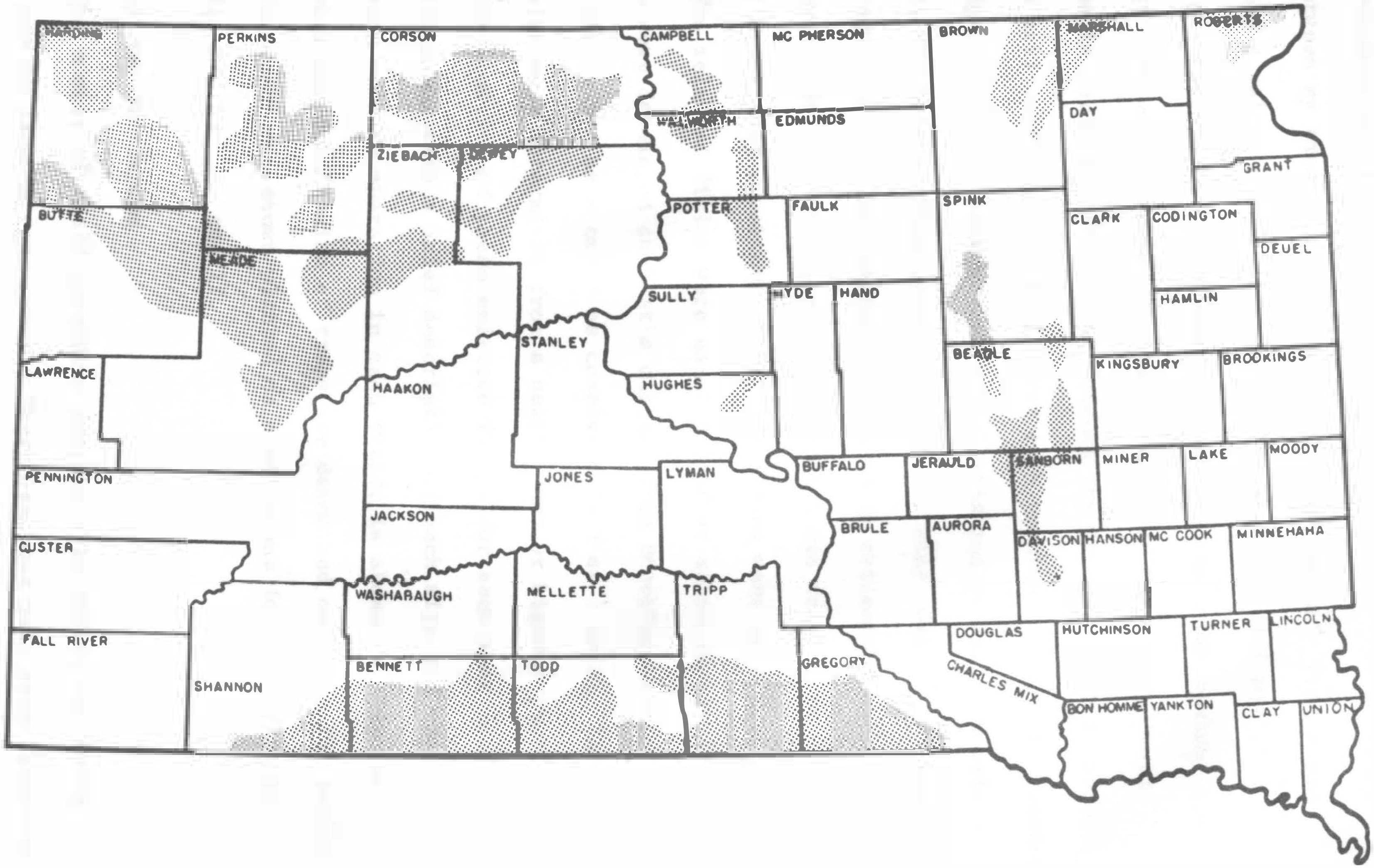
Fig. 10. The distribution of sandy loam and loamy sand soils in South Dakota (Westin and Buntley 1962a, 1962b).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by appearance and feel. When I rubbed the soil between my hands and between my thumb and fingers, sand particles felt gritty and silt had a talcum powder feel when dry. When the soil was wet, the plasticity could be estimated by rubbing the thumb against the sample: the more plastic the soil, the higher the clay content. Clay soils could also be rolled between the hands to form a "rope." If the soil held together well after such treatment, the clay content was high. Silt was only moderately plastic and sticky when wet. Persistent clodiness indicated high silt or clay content (Buckman and Brady 1966). These methods only gave an estimate as to the soil type, but the 4 classes of soil that I was interested in were so different that I believe my determinations were accurate.

The selected fields were usually near or along paved highways. Routes were developed so that a circuit from Brookings through western South Dakota and back could be completed in 2 or 3 days. The locations of fields were determined from a nearby town or highway junction.

The location of these selected fields for each year from 1964 to 1968, along with a brief description of each site and the dates the traps were in operation in each field, is shown in Addendum I. Placement and examination of traps are described on pages 201 to 212. Trap locations are shown platted on a state map for each year in Fig. 11, 12, 13, 14, and 15.

Results and Discussion

The number of field locations was variable within and among years due to farming operations. Therefore, the data from locations

Fig. 11. Locations of fields where false wireworm beetle populations were sampled - 1964.

1964

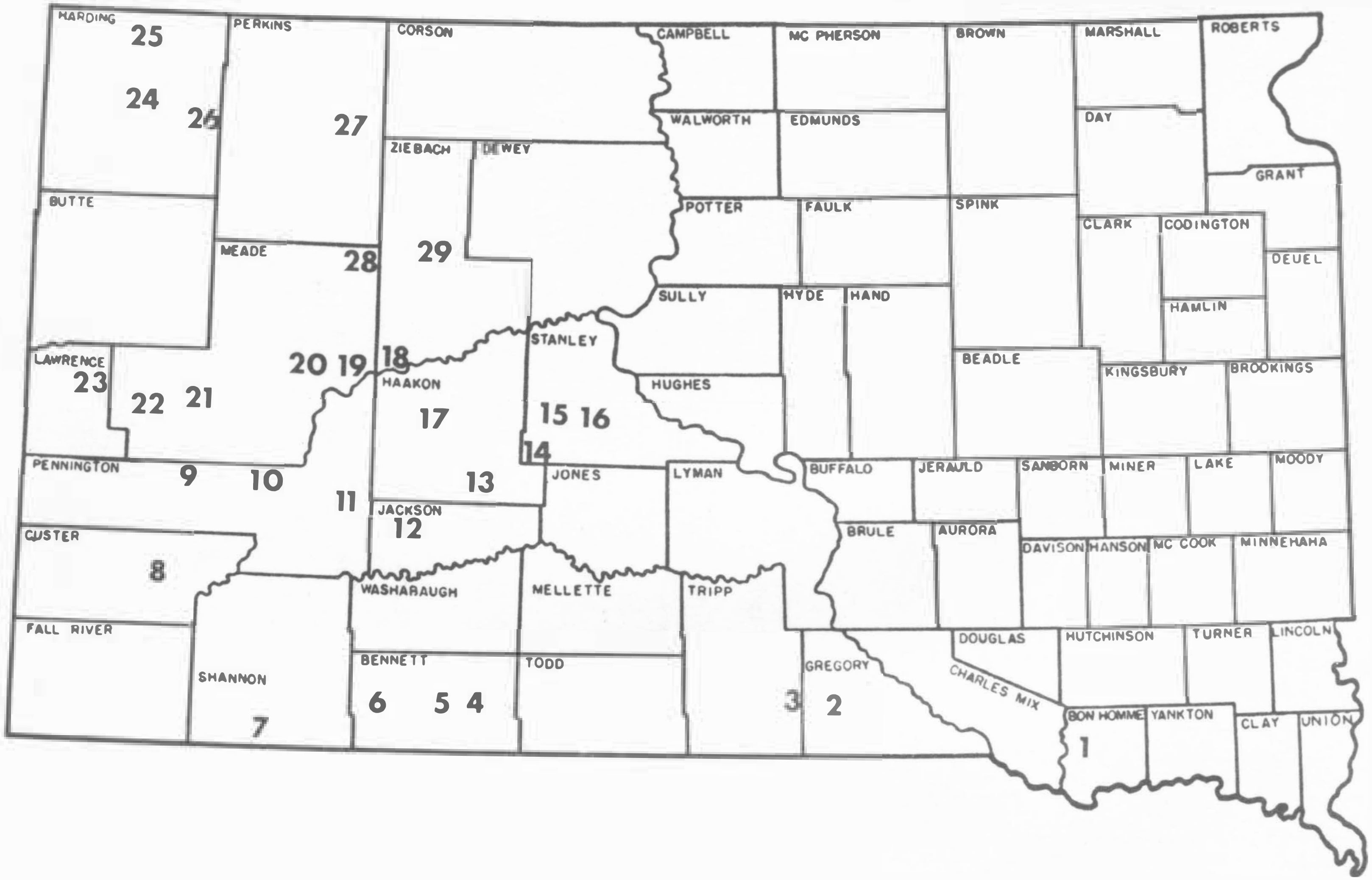
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Fig. 12. Locations of fields where false wireworm beetle populations were sampled - 1965.

1965

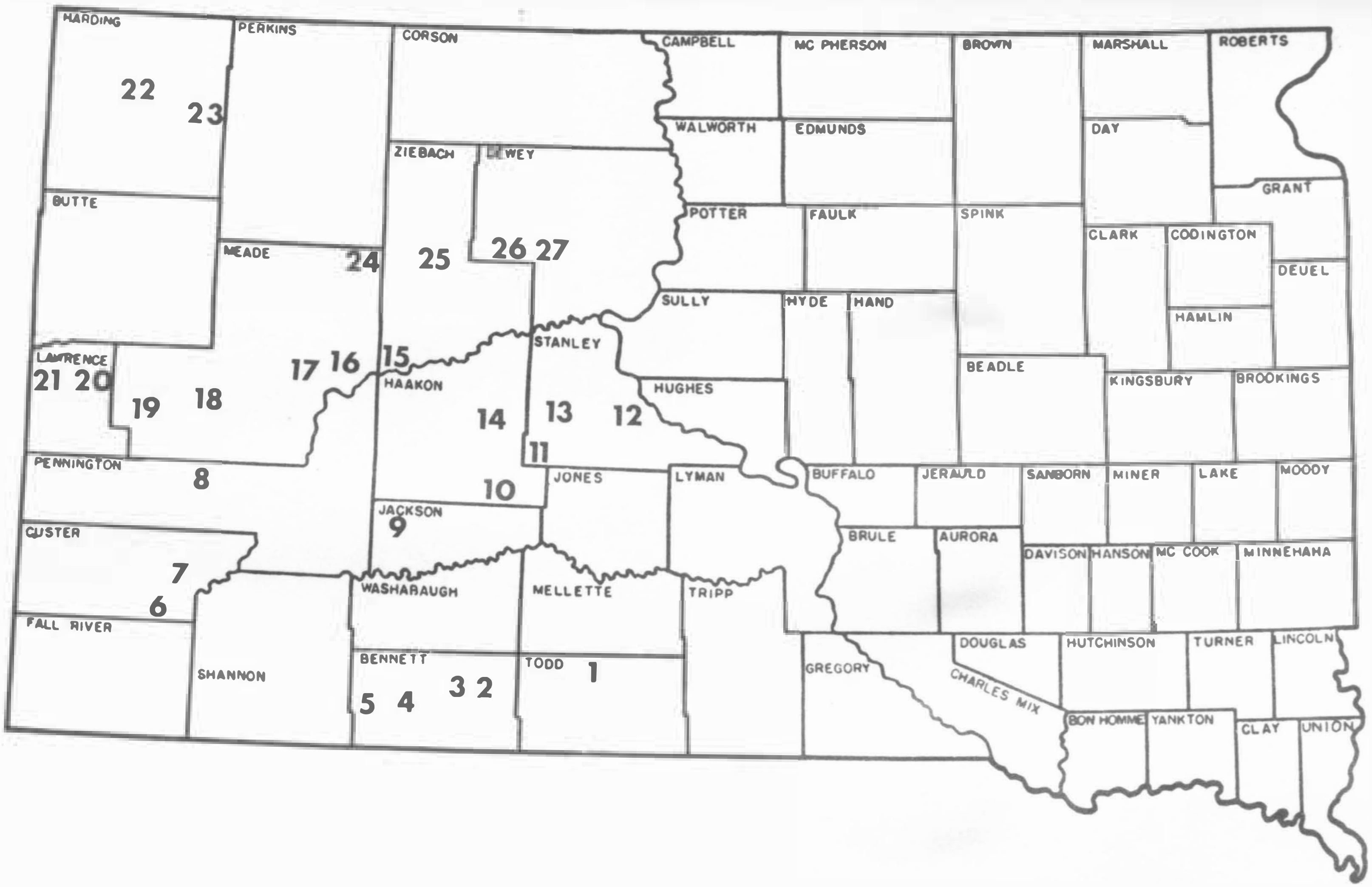
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Fig. 13. Locations of fields where false wireworm beetle populations were sampled - 1966.

1966

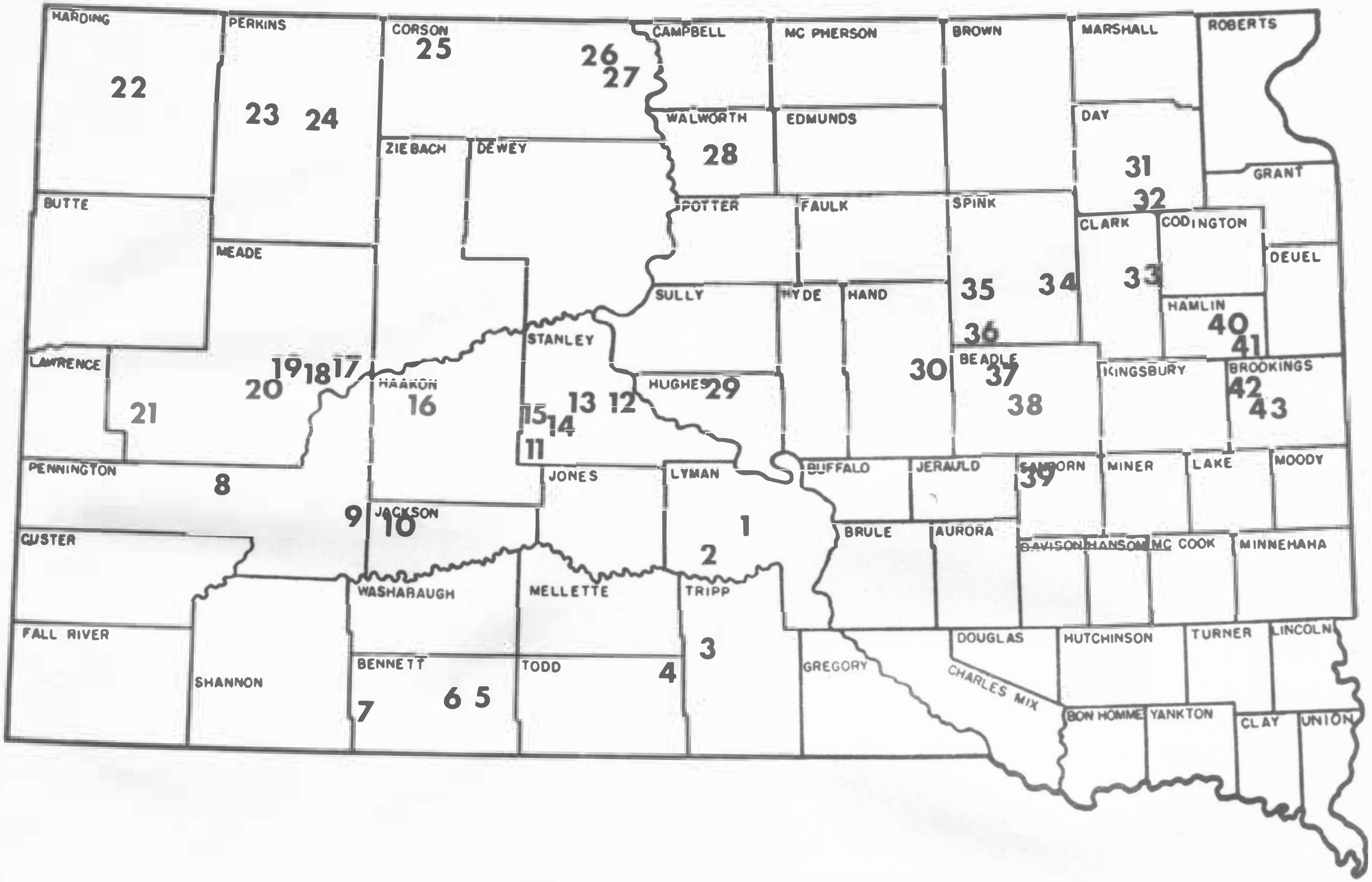
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Fig. 14. Locations of fields where false wireworm beetle populations were sampled - 1967.

1967

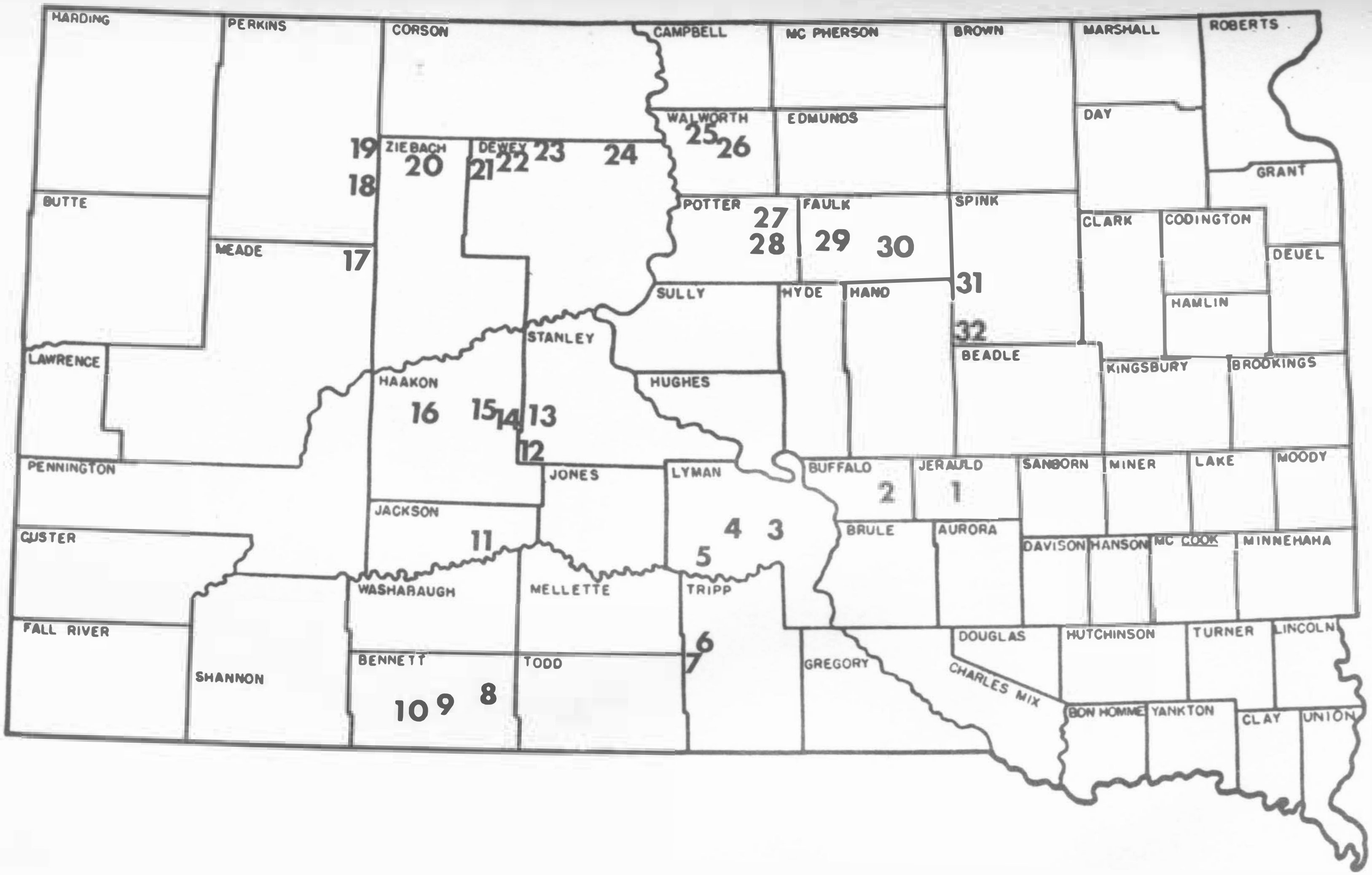
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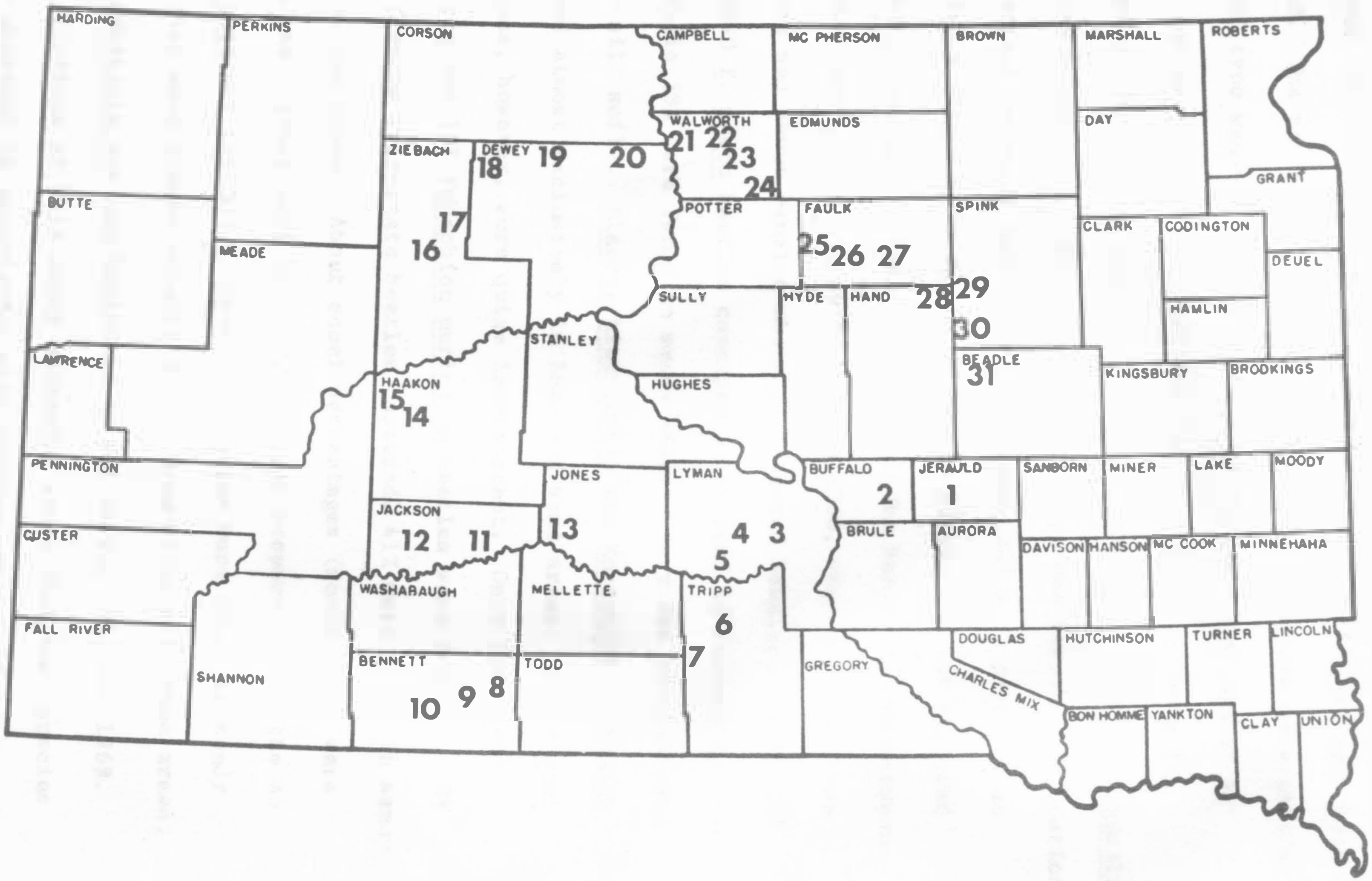
Fig. 15. Locations of fields where false wireworm beetle populations were sampled - 1968.

1968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having a particular soil type were adjusted to the number of beetles caught per 10 locations regardless of the actual number of locations involved. The percentage of beetles caught at locations of a particular soil type was determined in relation to the total number of beetles captured each year, and the data are shown in Table 15.

During the 5 years that this study was conducted, 869 E. suturalis beetles were captured. The largest percentage was trapped at locations characterized by sandy soils (49%); however, 24% were captured at sites with a clay soil. The least number of beetles was captured at locations having silt and loam soils. The beetle counts between treatments were consistent except during 1966, when all soil type treatments had about equal numbers of captured beetles. About 43% of the 2690 E. opaca beetles captured were found in regions of clay soils, while 38% were found in sandy areas. Very few beetles were found in silt soils. Eleodes hispilabris and Embaphion muricatum were found almost exclusively in loam and sand areas. The annual proportions, however, were quite inconsistent. Only 114 Eleodes hispilabris and 182 Embaphion muricatum beetles were trapped. Of the 298 Eleodes tricostata beetles captured, 41% were found in sandy regions of the state. About equal percentages (nearly 21%) were found in the 3 other soil types. Very high proportions of the 83 E. extricata and the 305 E. obsoleta beetles were found in sandy areas. They were almost totally absent from other soil-type areas. Eleodes extricata was not collected at all during 1967 and 1968.

The findings of this study generally agree that most species are more abundant in association with lighter soils. Eleodes opaca,

Table 15.--The percentage of false wireworm beetles trapped annually in clay, loam, silt, or sand soils in South Dakota, 1964-1968.

Year	% of beetles in each type of soil				Total no. beetles
	Clay	Loam	Silt	Sand	
			Eleodes suturalis		
1964	21	10	6	63	170
1965	24	8	12	56	240
1966	22	27	26	25	159
1967	32	18	6	44	157
1968	20	20	--1/	59	143
Mean	24	17	13	49	869
			E. opaca		
1964	28	37	1	34	175
1965	35	7	5	55	279
1966	65	10	7	18	746
1967	50	14	0	36	1080
1968	35	15	--1/	49	410
Mean	43	16	3	38	2690
			E. hispilabris		
1964	17	62	0	21	22
1965	2	2	28	67	31
1966	0	55	0	45	15
1967	2	25	0	73	32
1968	0	61	--1/	39	14
Mean	4	41	7	49	114
			E. tricostata		
1964	47	24	4	24	44
1965	26	57	5	12	76
1966	5	8	75	13	51
1967	2	15	0	82	76
1968	13	14	--1/	73	51
Mean	19	24	21	41	298
			E. extricata		
1964	0	0	0	100	21
1965	0	0	27	73	60
1966	0	0	0	100	2
1967	0	0	0	0	0
1968	0	0	--1/	0	0
Mean	0	0	9	91	83

Table 15.--Continued.

Year	% of beetles in each type of soil: Clay	Loam	Silt	Sand	Total no. beetles
			E. obsoleta		
1964	2	15	0	83	73
1965	0	8	9	83	125
1966	0	9	10	81	61
1967	0	10	0	90	21
1968	0	5	--1/	95	15
Mean	0.4	9	5	86	305
			Embaphion muricatum		
1964	3	61	15	21	16
1965	2	24	0	74	35
1966	0	80	0	20	11
1967	1	7	0	92	62
1968	0	48	--1/	52	58
Mean	1	44	4	52	182

1/ Grain fields having silt soil were not sampled in 1968.

however, was found abundantly in heavy clay regions several miles from sandy areas. The possibility that these flightless individuals migrated that far from the field where they developed is remote. Therefore, this species appears to have adapted quite well to these heavier soils. Eleodes suturalis and E. tricostata beetles were also found in abundant numbers on clay soils.

The economic importance of E. suturalis and E. opaca has been well documented. This hasn't been true of E. tricostata, however. Bruner (1892) observed it feeding on and damaging cabbage and other garden crops at Lincoln, Nebraska. Other workers (Blaisdell 1909, Wickham 1890, McColloch 1918) describe the feeding of this species as confined to weed and grass roots in native pastures. However, the number of beetles trapped in wheat fields in this study was quite high relative to some of the other species. The fact that it has not been found associated with damage probably indicates that if it can complete its life cycle in grain fields, most of the larval feeding is probably confined to roots where damage would be minimal. The possibility also exists that adults found in the grain fields had wandered in from surrounding grass borders.

The Effect of Soil Types on Growth and Survival of *E. suturalis* in the Laboratory

The effect of soil type on growth and survival of false wireworms was determined in the laboratory using larvae of *E. suturalis*. Soil samples were taken during September 1966 from 3 widely separated sites in South Dakota: (1) Perkins Co., 4 miles east of Bison, (2) Bennett Co., 3 miles west of Swett, and (3) Stanley Co., 3 miles east of Hayes. The soil types involved were loam, sandy loam, and clay, respectively. The fields that these soils came from had not been sprayed with insecticides in recent years. The samples were brought to the laboratory where they were 1st sifted through 1/4-in. hardware cloth to remove debris and then were placed in plastic bags to prevent drying. The bags of soil were stored at 4°C until used.

Galvanized metal pans (30.5X28X15.2 cm) were used to test the effect of soil type on larval growth and survival. Six pans were filled ca. 3/4 full, 2 each with each type of soil. Two hundred larvae together with ground wheat kernels were sprinkled over the soil surface of each pan. The pans were maintained at 27°C and 80-90% RH for 36 days, then all living larvae were extracted and counted to determine survival. The rate of growth of the recovered larvae was ascertained by measuring head capsule widths of 10 larvae selected at random from each pan.

Results and Discussion

There were 134 and 128 surviving larvae in pans containing sandy loam soil and 111 and 117 in pans containing loam soil. There were no living larvae found in pans containing clay. The rate of growth of larvae in both loam and sandy loam soils is shown in Table 16. The mean head capsule size was slightly less in larvae in sandy loam soil but the difference was not significant. All larvae were in the 8th instar.

The total lack of survival in clay soil was puzzling. There could be a number of contributing factors: insecticide contamination, some naturally occurring toxic chemical, disease organisms, lack of large pore spaces, etc. Clay soil in western South Dakota, even in summer fallowed strips, usually contains large amounts of plant debris that would create large pore spaces. The clay soil used in this experiment had been sifted to remove the larger plant debris. The soil then had a tendency to cake or compact with time. Also, the moist ground wheat became coated with fungus very rapidly. This phenomenon did not occur in the other 2 treatments: however, the larval activity kept the soil loose and friable at the surface and may have prevented conditions conducive to heavy fungal growth.

Table 16.--Rate of growth of E. suturalis in loam and sandy loam soils in the laboratory.

Larva no.	Head capsule measurements (mm)			
	Sandy loam		Loam	
	Replicate		Replicate	
	1	2	1	2
1	3.00	2.75	2.71	2.73
2	2.70	2.78	2.70	2.86
3	2.63	2.70	2.75	2.74
4	2.61	2.60	2.80	2.76
5	2.59	2.60	2.90	2.73
6	2.60	2.62	2.69	2.65
7	2.90	2.57	2.79	2.80
8	2.64	2.59	2.73	2.76
9	2.63	2.54	2.80	2.67
10	2.55	2.58	2.78	2.79
Mean	2.685	2.633	2.765	2.749

The Effect of Selenium on Growth of E. opaca and E. hispilabris larvae

There seemed to be a great disparity in the occurrence of some species of false wireworms with certain soils, particularly clay. The limiting factor in clay soils could be physical or chemical. The physical aspects would probably relate to structure or pore space, and the chemical aspects would relate to some compound or element unique to this type of soil. Such an element, selenium, is present almost exclusively in clay soils derived from Pierre shale.

Selenium is commonly found in certain soils of the Great Plains area of western United States. When it is absorbed and accumulated by plants that are in turn eaten in substantial amounts by warm-blooded animals, it causes severe complications and death. The symptoms have been referred to as "alkali disease" and the "blind staggers", both of which are misnomers. Selenium has also been shown to affect certain species of insects severely (Mason and Phillis 1937, Phillis and Mason 1938, Hurd-Karrer and Paas 1936, Nelson et al. 1933, Trelease and Trelease 1937), but Fox (1943) concluded that other insects are apparently able to resist its toxicity. He observed that many species of insects feed upon selenium indicator plants. The narrow-leaved milk vetch, Astragalus pectinatus (Hook.) Dougl. and the bisulcate milk vetch, A. bisulcatus (Hook.) A. Gray, commonly occur on selenium-bearing sediments and accumulate high levels of selenium within their tissues. These plants are fed upon by species of the following families: Cerambycidae, Cosmopterygidae, Elateridae, Curculionidae, Byrrhidae, Meloidae, Lycaenidae, and Bruchidae. Species of *Eleodes* were observed in the area but were not recorded as feeding on these plants.

Byers (1935) found that selenium in soil was more extensive in South Dakota than previously suspected. It was found coextensively with soils developed on Pierre shale, but its distribution was not uniform in surface soils or in the profile. However, its occurrence in vegetation was general wherever selenium was found in the soil. There appeared to be no relationship existing between topographic features and selenium content of vegetation. Pierre shale deposits and outcrops were listed from North Dakota, South Dakota, Nebraska, Montana, Wyoming, Colorado, and New Mexico. These areas constitute a large portion of the range of several species of false wireworms including some of those found in South Dakota.

Because certain portions of western South Dakota have soils high in selenium, the distribution of some species of false wireworms might be limited by the presence of selenium in the soil, and their distribution in relation to soil type may reflect this.

Of the species of false wireworms in South Dakota, *E. opaca* was the most common species found in areas of Pierre shale and *E. hispilabris* was one of the least commonly found species. In a preliminary experiment, these species exhibited a differential sensitivity to selenium when they were fed wheat containing moderate levels of this element, although both appeared somewhat tolerant. Because of these differences in response to selenium, an experiment was initiated to test the effect of selenium toxicity on growth and to determine whether selenium might be a factor in the distribution of false wireworms in clay soils.

Materials and Methods

The selenium used in these experiments was of the selenate form that is of organic composition as found in wheat kernels harvested from areas having high levels of selenium in the soil. Newly hatched larvae of E. opaca and E. hispilabris were weighed and placed in plastic disposable petri dishes (60X20 mm). Each dish contained 10 larvae and ground wheat containing 0, 11.4, or 34.0 ppm of selenium. Each treatment was replicated 5 times. Growth rates were determined by weighing the larvae each Monday, Wednesday, and Friday for 15-16 weeks. Mortality of larvae for each treatment was also determined.

Because these species were not as sensitive to levels of selenium as expected, the possibility that these larvae were able to avoid the toxic effects by not absorbing the material into their systems was examined. A preliminary test was conducted to see whether the larvae were absorbing, excreting, or metabolizing the selenium. Partly grown larvae were placed for 9-67 days in dishes of ground wheat having 34 ppm selenium. Larvae were removed for analysis throughout this period. They were 1st starved for 48 hr to assure that any traces of food had disappeared from the alimentary tract and then frozen for 24 hr at -17.6°C and placed in a freeze-dry apparatus (Virtis Freeze-Dryer #10-145 MRTR-SPBA) until all moisture was removed.

The sample was analyzed for selenium at the Station Biochemistry Department at South Dakota State University. The procedure they followed for analysis is as follows:

1. Samples were added to each of 5 microkjeldahl flasks.

2. Two glass beads were added to each.

3. 5 ml concentrated nitric acid were added to all flasks containing 0.5 g of sample or less, 10 ml of nitric acid were added to those containing larger samples.

4. To a 6th flask, 2 glass beads and 10 ml nitric acid were added. This served as the nitric acid blank.

5. The mixtures were allowed to stand at room temperature for at least 4 hr.

6. Air condensers were affixed and flasks were placed in a nearly upright position on the microkjeldahl digestion rack.

7. Flasks were heated slowly for ca. 5 min and then heating was increased until nitric acid condensed in lower part of the air condenser. They were then heated 10 min longer and then the burners were turned off.

8. When vigorous reaction had subsided, 2 ml perchloric acid were added through the air condenser in such a way as to wash down the sides of the condenser.

9. Flasks were swirled and refluxed during the 10 min.

10. The air condenser was removed and heating continued, fumes were drawn off in fume duct.

11. Heating was continued to perchloric acid fumes and then continued 15 min longer.

12. Apparatus was cooled and 1 ml water was added. Heating was resumed for 1-2 min beyond appearance of perchloric acid fumes.

13. 1.0 ml water was added to each flask.

14. A blank was prepared by measuring 1.0 ml water and 2 ml perchloric acid into a microkjeldahl flask.

15. A standard was prepared by measuring exactly 1.0 ml of selenium standard solution and 2 ml perchloric acid into another microkjeldahl flask.

16. All flasks were swirled, including the blank and standard, and 1.0 ml of ca. 2.5 N HCl was added with mixing.

17. Flasks were placed in vigorously boiling water bath for 20 min.

18. It was cooled to room temperature and 5 ml NH_2OH-EDTA solution and 2 drops cresol red indicator were added.

19. Approximately 5 N NH_4OH were added until a yellow color appeared. Then ca. 0.5 N HCl was added until an orange-pink color appeared. Put in 50°C water bath.

20. Shades were pulled and all but yellow lights were turned off. From this point on all manipulations were performed in semi-darkness or under yellow light.

21. Diaminonphthalene solution was prepared.

22. To each flask, 5 ml of the diaminonaphthalene solution and ca. 0.1 N HCl to the neck of the flask were added.

23. Each flask was mixed and placed in a 50°C water bath for 25 min (in the <u>dark).</u>

24. They were removed and cooled to ca. room temperature in a pan of water.

25. Mixtures were poured into 125-ml separatory funnels containing 10.0 ml decalin. Flasks were rinsed ca. 5 ml approximately 0.1 N HCl.

26. Flasks were shaken vigorously for 5 min, allowed to stand for a few min, and then were shaken again.

27. The fluorometer was turned on.

28. After the decalin has separated, the lower layer (usually containing a small amount of finely dispersed decalin) was withdrawn and discarded.

29. The decalin layer was washed for 1 min twice by shaking with 25 ml of approximately 0.1 N HCl, and the washings were discarded.

30. The decalin layer was transferred to 12-ml centrifuge tubes and centrifuged at moderate speed for a few minutes.

31. The decalin layer was poured into fluorometer tubes.

32. The fluorometer was zeroed against a tube containing only decalin, and then all the tubes (using the 1X position on the Turner fluorometer) were read.

33. The results were recorded and calculated.

This preliminary experiment showed that the selenium was being retained in the body tissue of the larvae. This raised the question as to whether the selenium was incorporated into specific systems. Larvae of both species were fed in the described manner for 3 weeks because previous findings showed that the element was absorbed and

Table 17.--Growth rate of <u>E. hispilabris</u> larvae fed ground seleniferous wheat.

	Larval weight (mg)		
Weeks	Control	11.4 ppm	34.0 ppm
0	0.34	0.34	0.35
1	.77	.85	.77
2	2.44	2.61	2.67
3	6.66	7.03	6.40
4	13.87	15.66	12.55
5	25.16	27.81	22.71
6	37.59	43.34	32.54
7	43.46	51.46	35.19
8	50.35	60.83	38.12
9	49.62	61.28	35.36
10	47.70	66.52	37.19
11	56.13	75.20	54.63
12	74.81	86.66	61.46
13	84.49	94.42	65.21
14	95.44	131.66	82.61
15	120.33	143.95	89.81
16	125.40	152.94	105.40
% growth compared to control	0	22	16
% mortality	92	78	82
	46/100	39/100	41/100

After 16 weeks, the growth rates of *E. opaca* were 51 and 24% greater on the moderate and high levels of seleniferous wheat, respectively, than the growth rates of larvae fed selenium-free wheat (Table 18).

Table 18.--Growth rate of *E. opaca* larvae fed ground seleniferous wheat.

Weeks	Larval weight (mg)		
	Control	11.4 ppm	34.0 ppm
0	0.45	0.46	0.46
1	.73	.83	.83
2	1.86	2.05	2.05
3	3.56	4.10	4.45
4	4.77	6.43	7.22
5	6.87	9.02	10.21
6	8.71	12.25	13.24
7	10.41	13.77	14.59
8	11.51	14.75	15.51
9	13.91	14.45	14.63
10	17.11	17.16	16.94
11	21.72	24.37	18.71
12	24.58	29.80	22.32
13	27.49	36.45	24.80
14	30.77	40.29	35.13
15	32.72	54.89	40.90
16	39.62	59.97	49.32
% growth compared to control	0	51+	24
% mortality	82	78	88

This experiment was repeated and the growth rates were 55 and 22% greater than the control on the same concentration levels (Table 19). The mortalities were identical and, like those of *E. hispilabris*, they were high (78-88%).

Table 19.--Growth rate of *E. opaca* larvae fed ground seleniferous wheat.

Weeks	Larval weight (mg)		
	Control	11.4 ppm	34.0 ppm
0	0.44	0.45	0.45
1	.74	.81	.82
2	1.82	2.04	2.17
3	3.46	4.00	4.48
4	4.68	6.31	7.20
5	6.82	8.98	10.16
6	8.54	12.13	12.52
7	10.07	13.62	14.10
8	11.23	14.52	15.05
9	13.86	14.34	14.76
10	17.23	16.87	17.16
11	21.28	22.50	20.20
12	25.08	28.19	25.09
13	28.20	34.29	28.17
14	31.48	38.63	35.45
15	32.55	55.46	42.47
16	40.06	62.04	49.06
% growth compared to control	0	55	22
% mortality	82	78	88

In preliminary tests, larvae of both species were shown to retain substantial amounts of selenium within their bodies (Table 20). The

Table 20.--Amounts of selenium retained within larvae of *E. hispilabris* and *E. opaca* that had fed upon seleniferous wheat.

Selenium in diet (ppm)	*E. hispilabris*	*E. opaca*
11.4	33.5	27.5
34.0	49.5	40.0
Control	1.0	2.3

individual parts of the body that were examined to determine the selenium content also showed substantial deposits (Table 21). The

Table 21.--Selenium content of various body parts of *E. hispilabris* and *E. opaca* that had been fed wheat containing 34 ppm selenate for 3 weeks.

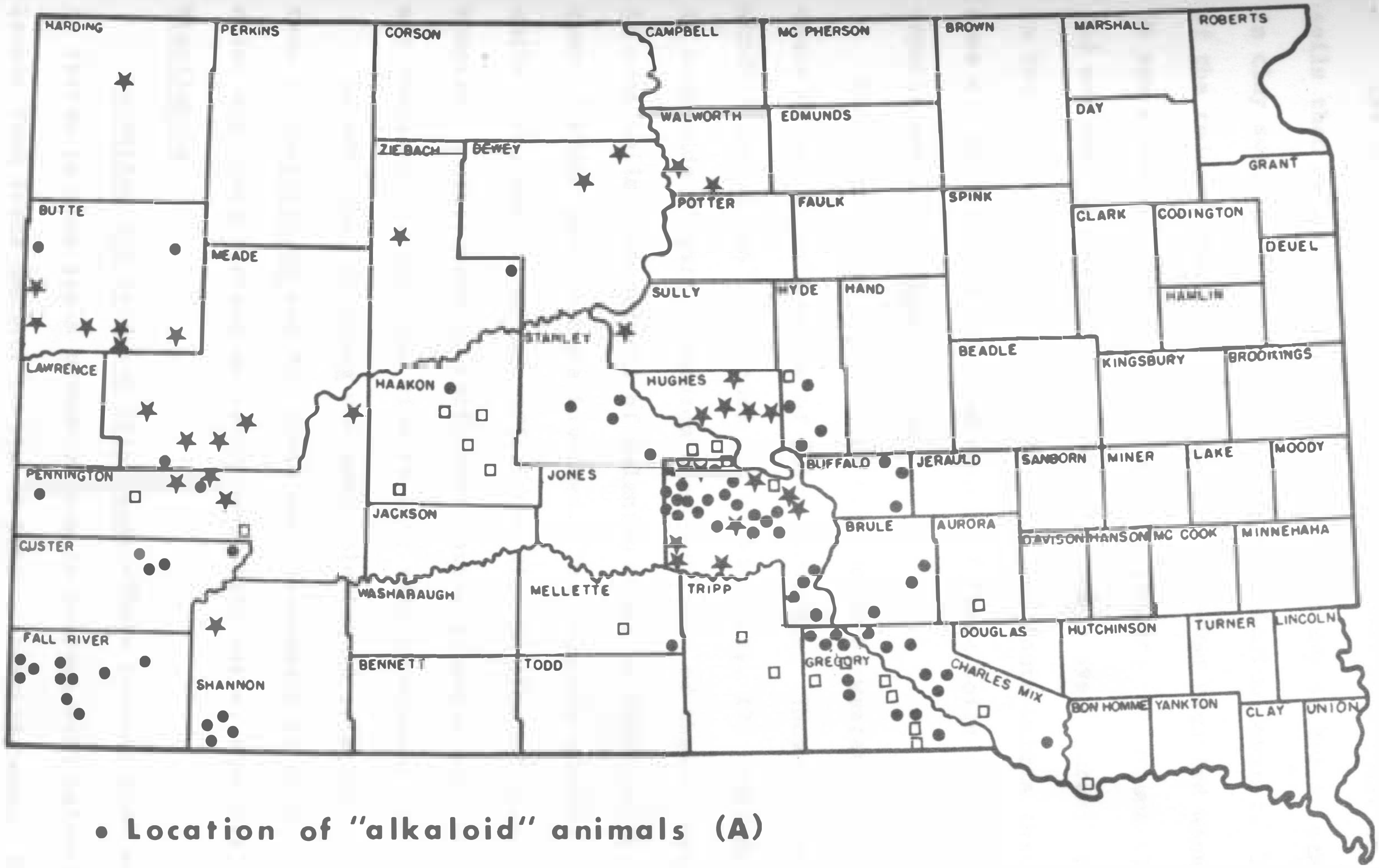
	Selenium content (ppm)			
	E. hispilabris		*E. opaca*	
Body parts	Control	Selenate	Control	Selenate
		Test 1		
Exuvia	4.8	56.2	1.0	21.6
Cuticle	5.6	9.5	2.9	16.3
Alimentary tract	10.0	83.2	0.8	60.0
Fat body	--	26.2	--	37.1
Excretia	2.2	65.9	.6	39.0
		Test 2		
Exuvia	1.1	58.9	1.1	33.9
Cuticle	0.9	20.1	.8	23.3
Alimentary tract	.8	70.0	.2	74.6
Fat body	--	35.3	--	35.9
Excretia	.8	68.8	5.5	47.3

highest levels of selenium were found in the alimentary tract. High concentrations were also found in the waste products passing out of the alimentary tract and in the cast skins, but much lower levels were present in the fat bodies and in the cuticle. Thus it appears that much of the selenium was in the process of being excreted. Because high levels were in the alimentary tract, it may mean that it also was in the process of being absorbed and relocated in the body. It is also possible that starvation for 48 hr, though long enough for the alimentary canal to empty, was not long enough for all of the selenium to be eliminated.

It seems that these larvae were able to ingest, tolerate, and excrete high levels of selenium. In fact, selenium even appeared to stimulate growth at lower levels. Eleodes opaca, however, appeared to have much greater tolerance to selenium than did E. hispilabris, especially at higher concentrations.

Distribution of Selenium Soils.--Soils containing selenium deposits in South Dakota are derived primarily from Pierre, Niobrara, Carlile, Greenhorn, and Granerous formations. Most cases of "alkali disease" were found on soils derived from Pierre and Niobrara formations. These soils include primarily the Pierre series, a clay soil covering extensive areas of western South Dakota (Fig. 8). The geographic distribution of selenium soils in South Dakota is generally limited to an area west of the Missouri River primarily in the south half of that part of the state (Moxon 1937). Figure 16 shows the geographic locations of positive selenium soil samples and the occurrence of "alkaloid" animals.

Fig. 16. Geographic occurrence of animals showing symptoms of selenium poisoning and of positive selenium soil samples: (A) location of farms on which "alkaloid" animals were observed by members of Experiment Station Chemistry Department, (B) location of farms on which "alkaloid" animals were observed by veterinarians (Moxon 1937).



• Location of "alkaloid" animals (A)

▫ Location of "alkaloid" animals (B)

★ Positive selenium soil samples

The distribution of E. hispilabris seems much lower on those soils than on nonseleniferous soils. This may be due to other factors in clay soil, or it could relate to the selenium content. In light of the reduced growth of E. hispilabris larvae when fed wheat having 34 ppm selenium, selenium does have an effect. Unfortunately, I did not test the effect of nonseleniferous clays on growth of larvae in the laboratory, nor did I find clays in South Dakota that I was sure did not contain selenium to see if these soils could have harbored populations of E. hispilabris.

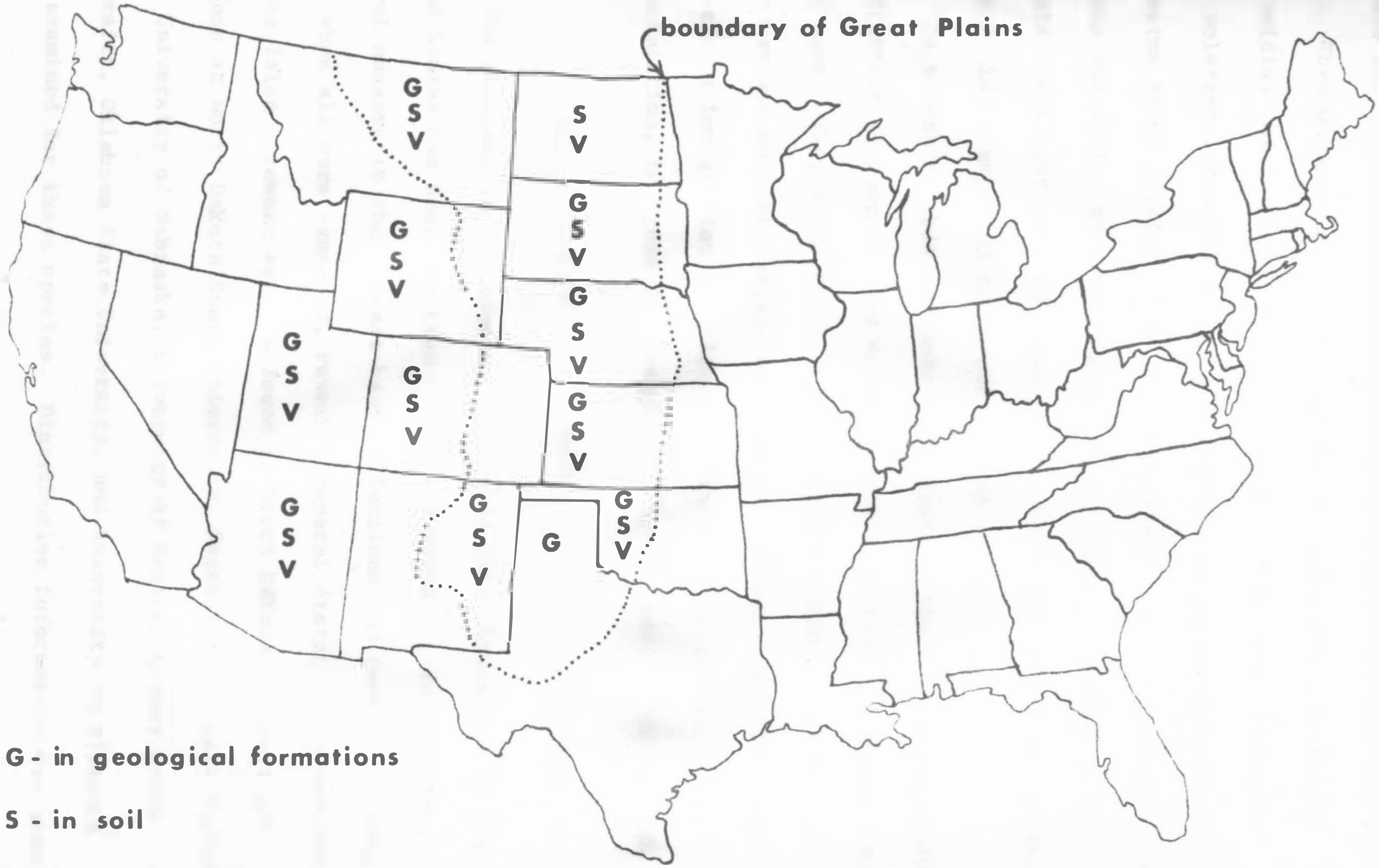
The presence of selenium in clay soils of western North America could affect other species of false wireworms. Those states in which selenium has been found are shown in Fig. 17. Because there is such wide disparity between the occurrence of these 2 species in clay soils, the effects of selenium would be expected to be greater than if other species were involved. The selenium content of clay soils alone may or may not affect the distribution of several other species. Unfortunately, sufficient larvae of other species were not available during this time to test this hypothesis in detail.

In any case, E. opaca was more tolerant of seleniferous wheat than E. hispilabris and was found more abundantly in clay soils, which are characterized as selenium-bearing soils, than was E. hispilabris.

Selection for Selenium Tolerance.--Those insects that are able to thrive in clay soils probably come in contact with selenium in levels from trace amounts to highly toxic concentrations. Those

Fig. 17. States in which selenium has been found in geological formations, soil, and vegetation (Moxon 1937).

STATES IN WHICH SELENIUM HAS BEEN FOUND



G - in geological formations

S - in soil

V - in vegetation

insects able to tolerate small amounts of toxicity survive and reproduce. Through many generations (probably hundreds), a mechanism of avoiding the toxic effects of this heavy metal was developed. This tolerance probably occurs and persists in populations of false wireworms found outside of seleniferous areas due to continual interactions and shifts of populations over distance. Although these insects are flightless, they are fairly mobil and over a few generations would be expected to spread several miles.

The genes for this mechanism of selenium tolerance would persist indefinitely as long as they were not detrimental to the insect in other ways. They would be diluted in the population, however, if there was not constant selection pressure for their presence, but if there is immigration of tolerant individuals continually into the population, the gene frequency would be maintained fairly high.

Distribution of False Wireworms on the Great Plains

The distribution of several species of false wireworms in the United States has been reported by several workers. In addition, several museums in the midwest have collections and records of captures that, when all were examined, revealed general distribution patterns for the false wireworm species found in South Dakota. Insect collections at North Dakota State University, South Dakota State University, University of Nebraska, University of Kansas, Kansas State University, Oklahoma State University, and University of Missouri were examined for these species. Distribution information was also secured from Plant Pest Control Division, ARS, U. S. Dept. of Agriculture.

All collection information secured during this dissertation, and incidental collections by V. M. Kirk and myself, specimen records from the above named institutions, and all collection information found in the literature were combined to produce distribution maps (Addendum II and III). County records were determined for the states of Colorado, Iowa, Kansas, Minnesota, Missouri, Montana, Nebraska, Oklahoma, South Dakota, and Wyoming. Species found outside of the Great Plains region, including Texas and New Mexico were only indicated as occurring in those states on a national map. The Great Plains were defined here as the extensive grassland biome from Texas to southern Alberta and extending eastward from the base of the Rocky Mountains for ca. 400 miles. These limits are generally defined in Fig. 17 (Moxon 1937).

Eleodes suturalis was recorded from 12 states, most of which comprised the Great Plains area. Collections were also recorded from Minnesota, Iowa, Oregon, and California. No specimens were recorded from Montana or North Dakota (Addendum II). *Eleodes opaca* was found in all of the Great Plains states except Wyoming. It was also found in Iowa. *Eleodes hispilabris* was collected in all of the western states except Nevada and appears to have the broadest distribution. *Eleodes tricostata* was found in all of the Great Plains states, in Idaho and Utah as well as in the tier of states immediately east of the Great Plains. The range of this species extends farther east than the other species, reaching somewhat into the subhumid and humid areas of the United States. *Eleodes extricata* was recorded from all of the western states except North Dakota, Washington, and California. *Eleodes obsoleta* was found throughout the Great Plains as well as in Utah and Arizona. *Embaphion muricatum* was found in all Great Plains states except Wyoming but was also recorded from Idaho and Oregon. *Glyptasida sordida, A. opaca,* and *A. polita* were collected infrequently in South Dakota, and their distributions were very restricted nationally: *G. sordida* was recorded from only South Dakota and Nebraska; *A. opaca* was recorded from South Dakota, Nebraska, Colorado, and Oklahoma; *A. polita* was recorded from Montana, South Dakota, Nebraska, and Oklahoma (Addendum II).

The county records for the states involving each of the 10 species are too extensive to treat narratively. The reader is therefore invited to refer to the state distribution maps in Addendum III.

These collection records probably are not complete, and the gaps in both county and state records do not necessarily mean that these insects do not occur there. Many insect collections that I did not have the opportunity to examine probably contain some of these species collected from locations that do not appear in these records. Probably no one has had the time or interest to collect specimens from these areas. This is demonstrated by the fact that many county records end at state borders.

One natural border that probably marks the eastern range of all of these species is the Mississippi River. Tanner (1961) did not find any collection records for false wireworms east of the Mississippi River. Records and specimens examined for this investigation did not refute his findings.

CHAPTER III

FACTORS RELATING TO FALSE WIREWORM DAMAGE

Wheat Culture in South Dakota

Winter and spring wheat are commonly grown in South Dakota under 3 cropping sequences: (1) continuously, that is, wheat grown on the same piece of land for several consecutive years, (2) in rotation with other crops (usually row crops), and (3) summer fallowing, which is the system most widely used in the semiarid portion of the state where false wireworms are most prevalent.

Summer fallowing was described by Rather and Harrison (1951) as a means of conserving moisture in semiarid regions, largely by elimination of moisture-consuming plants. The harrowed surface was also found to be more receptive to moisture than unharrowed surfaces. In addition, the stirring and aeration of the soil creates conditions favorable for nitrogen-fixing bacteria, and, in areas where leaching is not a factor, nitrates accumulate that are eventually used by the wheat crop.

The common practice for summer fallowing is to allow the grain stubble to stand from harvest until the following spring. The soil is then tilled, usually with a one-way disk before weeds begin to grow, and occasional tillage with various implements throughout the summer effectively controls weeds. The tillage also creates a mulch that further reduces evaporation from the surface. A savings of ca. 25% of the fallow season rainfall can be expected under most conditions (Buckman and Brady 1966).

Call and Salmon (1918) reported that disking immediately after harvest prevented the growth of weeds and conserved moisture for that same summer. Summer fallow was found to produce 10.7 bu of wheat more than continuous wheat at Hays, Kansas. They described another type of culture involving continuous wheat called "stubbling in." Ground that is loose and mellow can often be prepared for seeding with a disk, or wheat may even be sown in the stubble without any land preparation. The standing stubble protects the young wheat, catches and holds drifting snow, and prevents soil from blowing. This system was not recommended for several successive years because the ground surface gradually became harder each time it was used.

In an effort to extend the winter wheat growing area in South Dakota, researchers are advocating planting winter wheat in small grain or flax stubble (Anonymous 1968a, 1968b). Yields up to 48 bu/acre were realized in the Watertown-Garden City area where winter wheat survival during the winter is a problem. This technique used in conjunction with drought resistant varieties in the semiarid portions of the state would be the 1st step toward growing continuous wheat efficiently. If moisture is available in the fall, farmers may take a chance and plant winter wheat directly into the stubble. If the available moisture is sufficient to get the seedlings started, the stubble may retain enough snow to enhance the spring moisture levels and carry the crop through until normal spring and early summer rains.

Damage

The greatest injury by false wireworms was achieved by the larvae during the fall. They attacked fall seeded grain immediately after planting and destroyed it before germination. A single larva working along a drill was able to destroy several kernels (McColloch 1919, Swenk 1923, Wade and St. George 1923). Damage to individual kernels ranged from the ends being nibbled or just the germ eaten to the entire seed being consumed with only the husk remaining. Damage did not end when the seed germinated but continued until the seedlings had established good, vigorous root systems. When populations of larvae were high, intensive feeding frequently damaged young plants (Wade and St. George 1923, Srivastava 1955). McColloch (1919) observed larval damage to wheat seedlings several inches tall when larval populations were high. These plants were killed when larvae feeding on the epicotyl cut the plants off just above the seed.

The greatest injury occurred "almost invariably" during autumns when rainfall was abnormally low. During these dry periods, the seeds sometimes would not germinate for several weeks and were thus susceptible to injury for a longer period of time. During years when sufficient moisture was available for rapid germination, less damage was apparent (Wade and St. George 1923).

Infestations in the fall were often found spreading from the tops of knolls, thus giving the fields a spotted appearance. These areas were usually the driest parts of the fields and the wheat planted there was susceptible to feeding damage for a longer period of time.

Adults were observed feeding on wheat kernels scattered on the ground and even doing some injury to wheat heads in the "shock." However, the adult stage was not regarded as causing much loss. However, the adults, in being attracted to shocks, straw piles, and accumulations of grain, congregated to feed and remained to lay eggs. These areas were frequently the sites of intense larval damage to wheat the following year.

Fields that were most severely damaged had one or several things in common: damage occurred in fields in the vicinity of straw stacks, shocks, or scattered bundles of grain; weedy and trashy fields were heavily infested while fields with few weeds were not infested; summer-fallowed fields where poor weed control was maintained harbored larvae that destroyed newly seeded wheat; wheat planted on ground recently converted from pasture sod was severely damaged; wheat planted in fields in which wheat was destroyed the previous year was again attacked; and those fields in which wheat was grown consecutively for 2 or more years invariably was damaged (Hyslop 1912, McColloch 1919, Wade 1921, Swenk 1923, Wade and St. George 1923, Wakeland 1926, Srivastava 1955, Hamilton and Matteson 1966).

The percentage of loss by these insects could not be easily determined. McColloch (1919) found that farmers confused false wireworm injury with that caused by true wireworms, white grubs, fall armyworms, Hessian fly, and winter kill. Other workers reported farmers were not aware of damage during dry autumns until long after damage had occurred and the insects had vanished. By then, they attributed the damage to dry weather or to some mysterious plant disease. Damage usually occurred in large bare spots in the field, but in extreme cases, entire fields were destroyed. Wakeland (1926) estimated that Eleodes hispilabris probably caused ca. 10% annual loss to the wheat crop in Idaho.

The economic threshold was not determined, but Swenk (1909) observed populations of 3-4 larvae of E. opaca per ft of drill row damaging 60% of the wheat kernels. Personal observations of less than 1 larva/ft of drill row associated with damage observed in fields in South Dakota probably gives the closest estimate of an economic threshold available. Fields pictured in Fig. 18 and 19 had populations of 1 larva/ft of drill row in the severely damaged portions. B. H. Kantack (personal communication) indicated that treatment recommendations are not based upon larval numbers but upon the appearance of damage.

Because of the limited range and rate of movement of false wireworm larvae under the soil, the number of kernels destroyed by each larva would be small if kernels were detected solely by accident during random movements. It would thus take a very large population to cause economic damage in the short period of time between seeding and establishment of thrifty plants. Since this is not the case, these larvae probably detect the kernels before they come in direct contact with them. This probably is the result of some chemical

Fig. 18. Winter wheat field that had sustained ca. 60% loss of stand by *E. opaca*. Remaining plants were generally unthrifty (Haakon Co., S.D., 1968).

Fig. 19. Winter wheat field that had sustained damage by false wireworms. Dark patches are areas that escaped damage (Tripp Co., S.D., 1971).

associated with the kernel during germination. Calkins et al. (1967) demonstrated that larvae were able to detect germinating wheat kernels in the soil and to move toward them in olfactometer tests. Under natural conditions, chemical odors probably diffuse through the soil via the pore spaces and are absorbed by the soil water, thus producing a gradient radiating from the seed that attracts larvae toward it. Thus a single larva could move from 1 kernel to the next in the same drill row and destroy several kernels before the seedlings become established.

Artificial Infestations of *E. suturalis*

The economic threshold is defined by Stern et al. (1959) as "the density at which control measures should be determined to prevent an increasing pest population from reaching the economic injury level." False wireworms are economically important when their populations are at a certain level, depending upon moisture conditions at the time of seeding. When moisture is adequate for rapid germination, the larvae that are present have very little time to destroy the seeds or very young seedlings. However, when moisture is limited, germination is delayed and larvae have a longer period of time to feed; the result is that the same number of larvae are capable of destroying many more kernels and the economic threshold becomes lower. I attempted to establish economic thresholds using artificial infestations of *E. suturalis* larvae during 1965-1968.

Arrangements were made with Loren McMillan of Batesland, western Bennett Co., S. Dak., to artificially infest small portions of winter wheat fields immediately after the wheat was sown in September. Plots were located in different fields each year but never farther than 2 miles apart. The plot sites were on high level portions of the fields with good drainage, and the soil type was sandy loam. The wheat variety used each year was Lancer.

The study was designed to determine at what level of larval infestation economic damage would occur. To assure that damage was attained, a control plot and 3 high population levels were used: plots were infested with 0, 10, 20, or 30 larvae/ft^2 of soil. Each treatment was replicated 4 times. Each plot was 3X3 ft and was surrounded by a metal barrier (14 ga.) whose sides were 12 in. to prevent larvae from escaping (Fig. 20 and 21). The barriers were carefully set into the ground to a depth of 8-10 in. leaving ca. 2-4 in. extending above ground without disturbing the soil within. Plots were seeded during the second week in September in 1965, 1966, and 1967.

The test insects were 4th-instar larvae reared in the laboratory for 1-2 generations. Larvae were separated from the rearing media, counted, and placed in quart ice cream containers in increments of 10, 20, or 30 ca. 24 hr prior to being transferred to the field.

When the metal barriers had been set in place, a 3X3-ft frame divided into ft^2 sections was placed over each barrier (Fig. 22). Each ft^2 area was infested with the required number of larvae by

Fig. 20. Placement of metal barriers in soil for evaluating artificial infestations (Bennett Co., S.D.).

Fig. 21. Appearance of soil within the barrier before placement and after infestation.

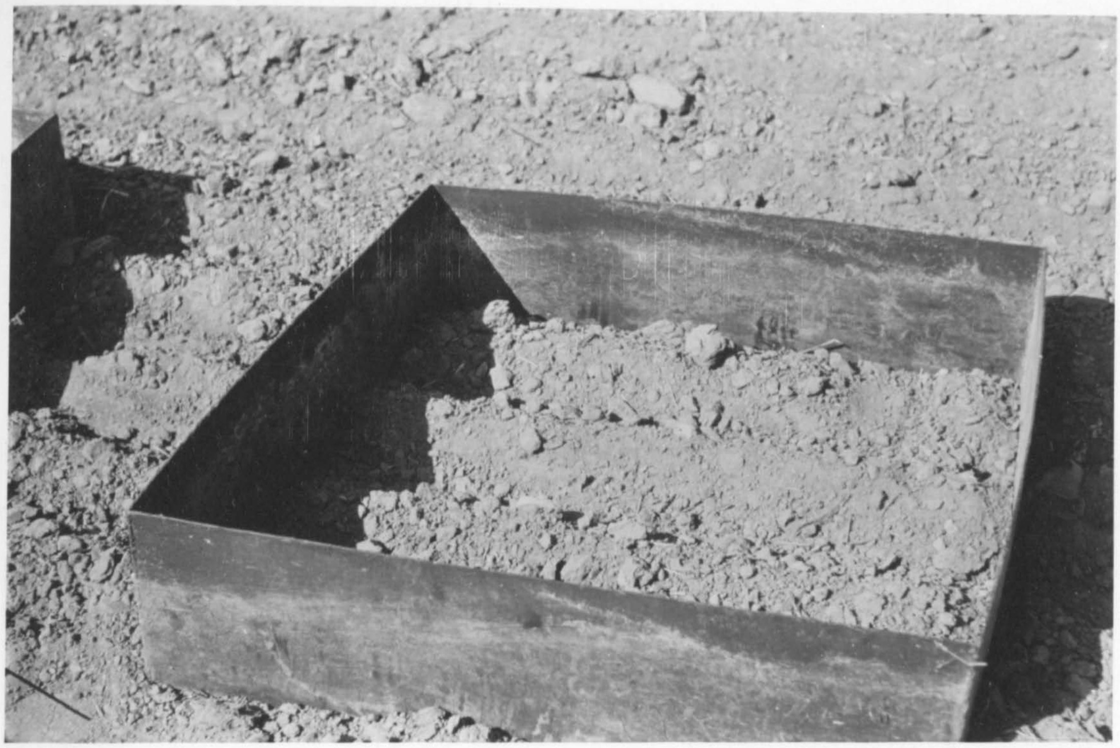
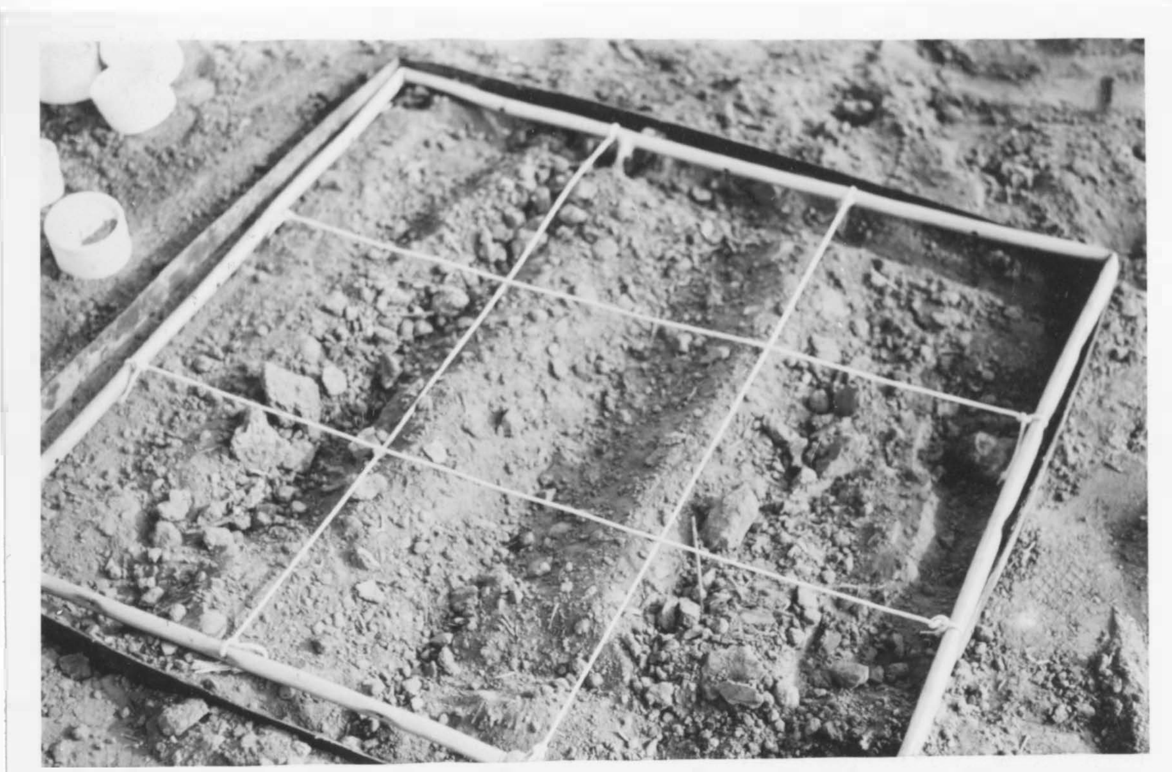


Fig. 22. Metal frame that divided plots into ft^2 sections to aid in infesting the plots with larvae.



excavating a small shallow hole between the drill rows and emptying the contents of a designated larval container into it. The larvae were then covered with soil and the surface was made to conform to its original condition as closely as possible.

After all plots had been infested, a watch was maintained over the plots for 1/2-1 hr to assure that birds would not immediately begin preying on the larvae before they could adapt to the new environment.

All plots were evaluated for damage by taking stand counts of wheat within the barriers ca. 1 month after wheat was sown. Because the rows in these fields were 14 in. apart, 3 rows, 3-ft long were included in each plot (Fig. 23). However, only the center 24 in. of each row was included in the stand count.

Additional evaluations were made the following spring during April to ascertain whether root feeding or partial damage to seedlings the previous fall may have weakened or killed the plants during the winter. Final evaluations were made when plots were harvested in July. The wheat was cut, placed in individual paper sacks, stapled shut, and returned to the laboratory. The total number of heads and the weight of threshed kernels were determined for each sample.

Jar-type pitfall traps were placed in the northwest corner within each barrier after the spring evaluation to trap emerging beetles. Adult counts would indicate how successful these laboratory-reared insects were in adapting to a field environment.

Fig. 23. Appearance of plant growth within barrier.

Results and Discussion

Dates of all evaluations are shown in Table 22. No harvest information was acquired during 1968 because the wheat was combined by custom operators before plots could be harvested. Stand counts,

Table 22.--Critical dates for evaluations of artificial infestations of *E. suturalis*.

	1965-1966	1966-1967	1967-1968
Plots seeded	Sept. 12	Sept. 11	Sept. 13
Plots infested	Sept. 13	Sept. 12	Sept. 14
Plants counted	Oct. 14	Oct. 12	Oct. 9
Winter kill evaluated	April 26	April 13	April 9
Plots harvested	July 20	July 25	-1/

1/ Plots harvested by farmer by mistake.

number of wheat heads, and yield data were analyzed by orthogonal comparisons (Steel and Torrie 1960) (Table 23). Three comparisons were made: (1) the check versus all infestations, (2) the lowest infestation rate with the 2 high infestation rates, and (3) the middle infestation rate with the highest infestation rate. The stand counts in the check plots were always higher than in the infested plots. However, there was a great deal of variability among the infested plots, although the plots infested with the highest number of larvae also had the lowest stand counts, the stand counts of the other 2 infestation rates were not consistent. In fact, plots having the lowest number of larvae also had stand counts that were equal to or lower than the plots having the next higher infestation rate.

Table 23.--Effect of artificial infestations of *E. suturalis* on stand counts, number of wheat heads, and yield.

	Infestation level (No./ft^2)	Stand count/6 ft row	No. wheat heads/6 ft row[1/]	Yield (g)/ 6 ft row[1/]
		1965-1966		
A.	None	52	395	217
B.	10	37	285	165
C.	20	37	325	209
D.	30	34	289	180
Orthogonal comparisons[2/]				
A vs B, C, D		*	*	*
B vs C, D		NS	*	*
C vs D		*	*	*
		1966-1967		
A.	None	40	316	328
B.	10	31	256	302
C.	20	32	254	299
D.	30	24	193	285
Orthogonal comparisons[2/]				
A vs B, C, D		*	*	*
B vs C, D		*	*	*
C vs D		*	*	*
		1967-1968		
A.	None	50	-	-
B.	10	44	-	-
C.	20	49	-	-
D.	30	42	-	-
Orthogonal comparisons[2/]				
A vs B, C, D		*		
B vs C, D		NS		
C vs D		*		

1/ Plots harvested by mistake in 1968.
2/ * = significantly different at 0.05 level of probability
NS = not significantly different.

No winter kill occurred to plants in the plots during the 3 years of study. Some winter kill that occurred in the county in 1967 and 1968 was caused by blowing soil that resulted in roots being exposed and/or leaves being damaged or cut off. Most such damage occurred on northwest and west-facing slopes and the cause could be readily identified. However, the plots did not suffer this fate.

There were significant differences in all comparisons for number of wheat heads and for yield. In the 1965-1966 study, there was a 15% reduction in yield when the check was compared to all of the infested plots. In the 1966-1967 study, the reduction in yield was 10%.

The highest number of adults was found in the 1st year of the study, and most of them were recovered from plots with the highest infestation rates (Table 24). There were 8 adults recovered from

Table 24.--Number of adults recovered from plots having been infested with designated numbers of larvae.

Infestation level (total no./treatment)	No. of recovered adults		
	1965-1966	1966-1967	1967-1968
0	8	0	0
360 ($10/ft^2$)	11	3	1
720 ($20/ft^2$)	23	2	1
1080 ($30/ft^2$)	34	5	2
Total	76	10	4

plots that had not been infested with any larvae. This indicates that there were larvae present in the soil before the barriers were inserted, that larvae were able to burrow under the metal barriers, or that "wild" adults were able to climb the barriers and get inside. If any of these possibilities were true, it casts doubts upon the value of these adult collections. However, only the 1st case would bias the results of the stand counts and other evaluations because the 1st month after seeding is the most critical for young plants. After that, any contamination would probably not affect subsequent evaluations because larvae have little effect on healthy vigorous plants.

The lowest infestation rate used in these studies was ca. 10 times larger than any natural infestation that I observed in the field. The 1st year, the rates were planned high to assure that differential damage would be apparent and also to achieve extremely high damage rates. When the damage appeared low and subtle, the high rates of infestation were continued for the next 2 years.

The low amount of damage caused by these high populations might be attributed to a number of factors. First, the larvae reared in confinement under constant ideal conditions may not adapt well to the outdoor environment. Secondly, the sudden change in environmental conditions possibly affected their behavior for several days and allowed enough time for the young seedlings to become established. The 3rd factor involves rearing insects in the laboratory and expecting them to behave and compete with "wild" insects under wild conditions. Even within 1 generation of rearing in the laboratory, the gene pool of the colony shifts drastically from the gene pool of "wild" populations. Severe selection pressure is exerted on the 1st generation for those individuals which adapt and survive in the rearing environment. Most insect colonies that are brought into the laboratory have difficulty in establishing themselves, at least during the 1st generation. After the initial generation, the rate of growth, successful completion of the life cycle, and the percentage of survival increase tremendously. This indicates that a laboratory colony has now been established that possibly cannot readily readapt to field conditions.

The total reduction in stand by the artificial infestations was 31 and 28% for the fall of 1965 and 1966, respectively. The reduction in yield was only 15 and 10% for these 2 years. When plants are removed in a very discontinuous manner, the reduction in yield is not closely correlated to the reduction in numbers of plants since surrounding plants then use the additional water, space, nutrients, and light to increase their yields. This is especially true when the supply of any of these items is limited. Therefore, for false wireworms to be economically damaging, their damage should be somewhat continuous to produce significant gaps in the drill rows.

Food Preferences of *Eleodes suturalis* and *Embaphion muricatum*

False wireworm larvae have been reported to feed upon seeds of wheat, native grasses, oats, corn, rye, millet, alfalfa, kafir, and weeds. Many authors have indicated that wheat is the preferred host when the insect has a choice. Other materials that have been implicated as larval food include potato tubers, fleshy roots of sugar beets, garden plants, dead organic matter, and roots (McColloch 1919, Wade and St. George 1923, Hyslop 1912). Adults were reported to feed on such plant leaves as evening primrose and Russian thistle (McColloch 1919, Swenk 1923). Srivastava (1955) reported that *Eleodes suturalis* feeds only on seeds and never on seedlings. Webster (1912) reported *E. suturalis* feeding on chinch bugs.

Larval damage to wheat usually occurs from the time it is planted until it germinates and develops a vigorous root system. Damage occurs when larvae attack the germ of the seed, eat the internal parts, and leave the hull behind. Apparently, the larvae detect a chemical emitting from germinating wheat kernels and are attracted toward them (Calkins et al. 1967). Murray (1960) reported that *Tenebrio molitor* responded to a true feeding stimular in bran, which was not nutritionally adequate. The response was not evoked by simple proteins, carbohydrates, or fats. Apparently, the attracting substance was an integral part of the cereal kernel. When the insect located it, it also located the entire food morsel. Therefore, the system of host finding did not have to be complex.

False wireworms have been identified as pests of planted grains and other crops in the Great Plains area of the western United States. Although wheat was reported as being most severely damaged and seemed to be preferred by many of the species, no one has ever evaluated the response of any species to choices of different seeds. Damage to grain is often difficult to attribute to any 1 species when several species may be present concurrently in a field. Although several species may be present, they may not necessarily all be feeding upon wheat but may, in fact, prefer other seeds or material occurring in the soil.

Food preference studies were conducted with 2 species (*E. suturalis* and *Embaphion muricatum*) that were being successfully mass reared in the laboratory and were sufficiently plentiful to use in large numbers in replication. These studies were designed to determine the food preferences for seeds of common native and introduced plants and to evaluate the potential danger from these insects to newly seeded crops.

Materials and Methods

Seeds from the following 34 types of plants (representing 31 species) were evaluated for preference of *Eleodes suturalis*. These same species with the exception of goat's-beard, plantain, and Harding grass were used in tests with *Embaphion muricatum*. Grasses and broadleaf plants were classified from Hitchcock (1950) and Fernald (1950), respectively.

Common name (variety name)	Scientific name
Alfalfa (Ranger)	*Medicago sativa* L.
Barley (Omugi)	*Hordeum vulgare* L.
Hulless barley (666)	*Hordeum vulgare* L.
Big bluestem	*Andropogon gerardi* Vitman
Corn	*Zea mays* L.
Crested wheatgrass (Fairway)	*Agropyron cristatum* (L.) Gaertn.
Flax (Summit)	*Linum usitatissimum* L.
Forage sorghum (Sorghum Dual)	*Sorghum bicolor* (L.) Moench
Goat's-beard	*Tragopogon* sp.
Grain sorghum (Reliance)	*Sorghum bicolor* (L.) Moench
Green foxtail	*Setaria viridis* (L.) Beauv.
Green needlegrass	*Stipa viridula* Trin.
Harding grass	*Phalaris tuberosa* var. *stenoptera* (Hack.) Hitchc.
Indiangrass	*Sorghastrum nutans* (L.) Nash
Johnsongrass	*Sorghum halepense* (L.) Pers.
Kentucky bluegrass	*Poa pratensis* L.
Little bluestem	*Andropogon scoparius* Michx.
Oats (Clinton)	*Avena sativa* L.
Hulless oats (James)	*Avena sativa* L.
Plantain	*Plantago* sp.
Russian wild rye	*Elymus junceus* Fisch.
Rye (Caribou)	*Secale cereale* L.
Sand bluestem	*Andropogon hallii* Hack.
Sand lovegrass	*Eragrostis trichodes* (Nutt.) Wood
Side-oats grama	*Bouteloua curtipendula* (Michx.) Torr.
Smooth brome (Homestead)	*Bromus inermis* Leyss.
Soybean	*Glycine max* (L.) Merr.
Sudangrass (Piper)	*Sorghum sudanense* (Piper) Stapf
Sugarbeet	*Beta vulgaris* L.
Sweetclover	*Melilotus officinalis* (L.)
Switchgrass	*Panicum virgatum* L.
Western wheatgrass	*Agropyron smithii* Rydb.
Wheat (Minter)	*Triticum aestivum* L.
Yellow foxtail	*Setaria lutescens* (Weigel) Hubb.

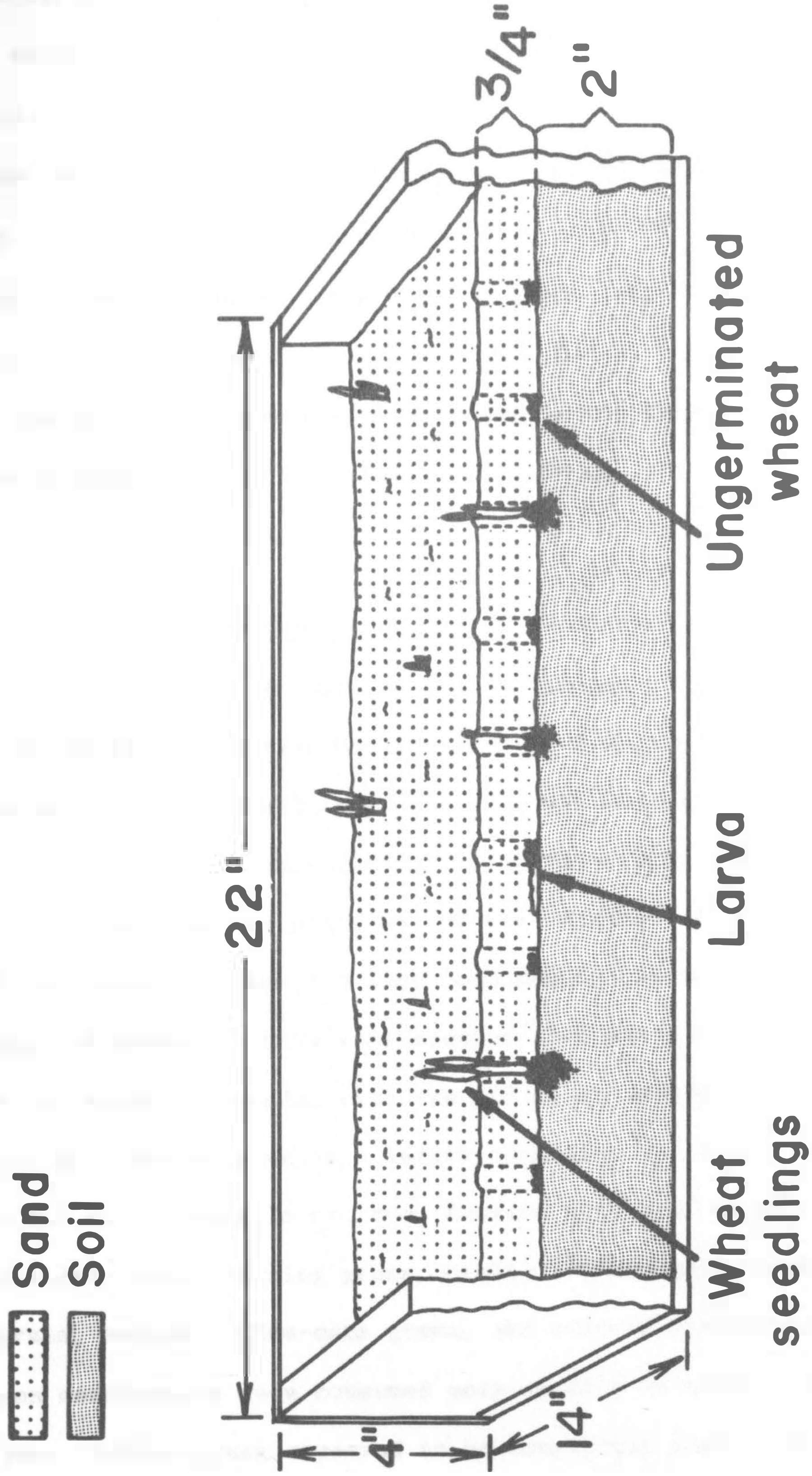
Almost all of the native and introduced range grasses recommended for western South Dakota rangelands were included in this study (Derschied et al. 1966).

Laboratory Tests.--The food-preference tests in the laboratory were made with adults and with 5th and 6th instars obtained from field collections and 1st-generation rearing. Test chambers consisted of covered aluminum containers (10X15X7.6 cm) used regularly in a false wireworm-rearing program like the one described by Matteson (1966a, 1966b). Moist sand less than 1 mm deep provided a rough surface for traction and proper humidity for testing. It was established in preliminary tests with Eleodes suturalis that an adult consumed ca. 5 kernels of wheat/day after it had been starved for 24 hr; a similarly treated 6th instar consumed ca. 4 kernels/day. Then, 5 insects, starved for 24 hr, were placed in each chamber with 5 kernels of Minter wheat and 5 seeds each of 2 other plants. Fifteen such combinations of seed with wheat seed as the control were tested. When little or no feeding occurred in a test, that test was eliminated, and those insects were not used in subsequent tests. Preferences were rated by the percentage of seeds of each type consumed in 24 hr. Embaphion muricatum, a species smaller than Eleodes suturalis and with a lower rate of food consumption, was tested for 48 hr under the same conditions.

Greenhouse Tests.--Since larvae are normally underground when feeding, a greenhouse test was designed in which several food sources were provided at conditions that allowed the larvae to burrow. Thus, wooden greenhouse flats (55X36X10 cm) were filled with potting soil (a mixture of peat moss, sand, and clay loam soil) to a depth of 5 cm, and ca. 1.9 cm of sand was layered on top and pressed down with a flat board. The flats were then placed in shallow pans containing ca. 3 cm of water so the soil and most of the sand became saturated. After ca. 1 hr, the flats were removed from the pans, the excess water was allowed to drain off, and a plywood board (54X35 cm equipped with 54 19X6-mm pegs arranged in 6 rows of 9 pegs each) was pressed into the sand to form 54 holes 5 cm apart that reached to the sand-soil interface (Fig. 24).

Three types of grain seed were planted in each prepared flat in a random distribution with 2 seeds of the same kind in each hole. One type (Minter winter wheat) always served as the check, since the rate of feeding on this seed was well established and could be used to determine the effectiveness of the larvae. The holes were filled with sand, and the surface was compacted again. The site of each type of seed was identified by a different colored toothpick. This technique placed the seed at the interface between soil and sand, which was also the interface between moist and dry media, a location where I have most often found larvae in field soil. Then 50 4th-instars of *E. suturalis* or 50 6th-instars of *Embaphion muricatum* were introduced into shallow slits in the sand between rows and were covered with sand to encourage them to burrow rather than to crawl on the surface.

Infested flats were maintained in the greenhouse at 24°C for 8 days until the germinating plants emerged above the sand and vigorous root systems developed, precluding accurate evaluations of feeding damage. Damage was evaluated by observing the number of undamaged shoots above ground. If shoots were missing, the immediate area was excavated to see whether the seeds had been damaged or had simply


3/4"
2"
22"
Ungerminated wheat
Larva
Wheat seedlings
4"
14"
Sand
Soil

not germinated. Larvae were recovered and counted after each test. If more than 5 larvae were missing, the data from the flat were discarded.

Each test was replicated 6 times, and the entire study was repeated 3 times with the species of seed in different combinations each time. Two additional flats without larvae served as checks.

The technique did not lend itself well to the evaluation of feeding preferences of small seeded plants, since they normally are not sown as deeply nor is germination as uniform.

Results and Discussion

Laboratory Tests.--Eleodes suturalis.--Table 25 shows results of the laboratory feeding tests as the percentage of seeds damaged. Feeding by adults and larvae was compared in a total correlation after an arcsin transformation of the data was made (Steel and Torrie 1960). A high positive correlation (0.736**) existed between larval and adult preferences for all types of seed tested. Thus, 90% or more of the seeds of 9 species were consumed by larvae, and a large percentage of seeds of these same species also was consumed by adults (except for seeds of Russian wild rye and smooth brome).

Usually, larvae consumed a larger percentage of seeds than did adults; e.g., sweetclover, rye, Russian wild rye, smooth brome, green foxtail, corn, Harding grass, crested wheatgrass, sudangrass, switchgrass, soybean, side-oats grama, and western wheatgrass. Oats and green needlegrass were consumed more readily by adults than by larvae. Indian-grass appeared to be completely immune to feeding

Table 25.--Percentages of seed of various plants eaten by larvae and adults of E. suturalis in laboratory tests.1/

Plant species	% seeds consumed by Larvae	Adults
Hulless barley*	100	95
Hulless oats*	100	96
Wheat*	99	92
Forage sorghum*	98	85
Grain sorghum*	98	100
Sweetclover*	96	64
Rye*	92	73
Russian wild rye*	91	3
Smooth brome*	90	14
Alfalfa*	79	94
Flax*	76	93
Green foxtail*	75	16
Corn	71	45
Harding grass*	61	13
Oats*	58	78
Crested wheatgrass*	53	13
Sudangrass*	43	14
Barley*	41	49
Switchgrass	38	7
Soybean*	36	9
Sand lovegrass	28	14
Side-oats grama	27	0
Western wheatgrass	23	1
Big bluestem	19	1
Plantain*	19	34
Green needlegrass	18	80
Kentucky bluegrass*	17	16
Johnsongrass*	14	2
Sand bluestem	8	0
Sugarbeet	8	3
Yellow foxtail*	6	14
Little bluestem	4	7
Goat's-beard	2	3
Indiangrass	0	0

1/ Based upon 15 tests.
* Introduced species.

by both adults and larvae.

Embaphion muricatum.--Feeding of these adults and larvae was also compared in a total correlation following an arcsin transformation of the data. Seed preferences of larvae and adults were very similar (correlation coefficient 0.896**). Adults consumed a higher percentage of seeds than larvae with a few exceptions (Table 26). Most of the preferred plant foods were introduced species. The native grasses, except for sand lovegrass and side-oats grama, did not sustain even moderate feeding. Green foxtail was preferred much more than yellow foxtail. Seeds of yellow foxtail are larger but appear to have a harder seed coat which possibly discouraged this insect from feeding on it.

Greenhouse Tests.--Eleodes suturalis.--No germinating seeds appeared to be immune to feeding damage (Table 27). Sugarbeet seeds, which were practically immune in the laboratory tests, were the most heavily damaged of all crop seeds tested and were almost completely consumed. Intact sugarbeet seeds appear hard and have a rough, thick seed coat that may prevent feeding, but they probably became susceptible when they germinated. Corn and soybeans were the least damaged, but such large seeds may require more extensive feeding before damage occurs.

Hulless barley and hulless oats were fed on more heavily than the hulled types, which was in agreement with the results of the laboratory tests with larvae. Barley and oats were preferred about equally in laboratory tests, but barley was damaged somewhat more in greenhouse tests than in laboratory tests.

Table 26.--Percentages of seed of various plants eaten by larvae and adults of E. muricatum in laboratory tests.1/

Plant species	% seeds consumed by Larvae	Adults
Wheat*	66.6	79.2
Hulless oats*	65.0	85.3
Rye*	56.0	89.3
Green foxtail*	45.0	52.0
Sweetclover*	41.0	72.0
Grain sorghum*	40.0	56.0
Forage sorghum*	35.0	55.0
Hulless barley*	33.3	50.6
Alfalfa*	29.6	74.4
Sand lovegrass	24.0	66.7
Corn	21.0	36.0
Side-oats grama	20.0	10.7
Kentucky bluegrass*	17.7	20.0
Oats*	17.6	6.0
Smooth brome*	17.0	14.7
Crested wheatgrass*	15.0	9.0
Barley*	11.0	8.0
Flax*	9.3	14.7
Russian wild rye*	8.0	29.0
Switchgrass	7.0	4.0
Big bluestem	5.3	6.7
Green needlegrass	5.3	2.7
Johnsongrass*	4.0	10.0
Little bluestem	2.7	9.3
Sand bluestem	2.7	1.3
Western wheatgrass	2.7	1.3
Yellow foxtail*	2.7	4.0
Sudangrass*	1.3	10.7
Soybean*	1.0	2.0
Indiangrass	0	5.3
Sugarbeet	0	2.7

1/ Based upon 15 tests.
* Introduced species.

Table 27.--Percentage of plants damaged by larvae of *E. suturalis* in greenhouse tests.1/

Crop species	% loss of seeds and seedlings
Sugar beet	100.0
Hulless oats	95.9
Forage sorghum	94.9
Grain sorghum	93.2
Hulless barley	83.5
Wheat	71.6
Rye	70.7
Flax	64.1
Barley	57.2
Oats	54.5
Corn	39.2
Soybeans	26.4

1/ Based upon 3 tests each with 6 replications.

Wheat was not damaged as much when it was germinating in soil in the greenhouse as when it was offered in pans in the laboratory. Thus, the rapid germination and establishment of a vigorous root system characteristic of this plant species, enabled it to escape damage by shortening the time during which it was susceptible. However, in general, a larger percentage of seeds was consumed in laboratory tests than in greenhouse tests: in the laboratory, the rate was 3 seeds/larva per day; in the greenhouse, it was 0.27 seeds/larva per day. Of course, in laboratory tests, the insects were confined to a small area with the seeds, but in greenhouse tests the larvae had to search for the seeds much as they would in the field.

Embaphion muricatum.--In the greenhouse test, rye and wheat were more severely damaged while barley, soybeans, and oats were only moderately damaged (Table 28). Germinating soybean seeds were

Table 28.--Percentage of plants damaged by larvae of *E. muricatum* in greenhouse tests.1/

Crop species	% loss of seeds and seedlings
Rye	67.2
Wheat	50.0
Barley	24.1
Soybeans	21.3
Oats	20.4

1/ Based upon 3 tests with 6 replications.

more susceptible in the greenhouse test than when intact seeds were exposed to larvae and adults in the laboratory. Seedlings were killed by damage to the radicle, hypocotyl, and cotyledons. Soybean seeds that failed to germinate showed little or no feeding.

In the field, winter wheat and rye are most susceptible during dry autumns when germination is retarded. Apparently, such conditions allow the false wireworm larvae more time to feed on plants in the seed and seedling stages. Most other crops are sown in the spring when moisture is more favorable to growth, but occasionally, in the semiarid portion of the Great Plains, the spring weather is dry and seeds do not germinate rapidly. Thus, if false wireworms are present, damage could certainly occur.

Crops that are adapted to dryland conditions and are susceptible on the basis of being preferred food include forage and grain sorghum, wheat, rye, flax, oats, and barley, with the hulless varieties of oats and barley being more susceptible. However, the extent of damage done to these seeds would depend on the insect population present, the moisture level of the soil, and the previous year's crop involved. For example, corn and sugarbeets usually are grown under irrigation in dryland areas. Therefore, if these crops were planted in a field that had been in sod or small grain the year before, false wireworm larvae might well be present, and these crops could sustain damage. Also, small-seeded legumes and grasses that are normally planted shallowly could be attacked by both larvae and adults; e.g., sweet-clover, alfalfa, Russian wild rye, smooth brome, Harding grass, crested wheatgrass, and green needlegrass.

Some seeds in the tests did not appear acceptable as food. They may sustain the insect under starvation conditions, but it is doubtful whether the percentage of seeds sown would be reduced significantly.

This study has shown that introduced plant species were preferred as hosts over native species. Because seeds of most of the evaluated crop species were severely damaged, we must consider both *Eleodes suturalis* and *Embaphion muricatum* potential economic pests of crops grown in the Great Plains under dryland conditions.

Control

Control of false wireworms has always been a problem. Some of the control measures used in the past consisted of mechanical, cultural, and chemical methods. Mechanical control was often applied after damage had occurred and probably didn't protect the crop being damaged. Cultural control usually was applied as a prophylactic treatment and involved a change in farming methods on a regular basis, whereas the insects may have been important only on an intermittant basis. The cost of chemicals to protect the crop sometimes exceeded the damage that would have resulted with no control.

Mechanical Control

Most of the mechanical control procedures involved plowing to destroy pupae. Hyslop (1912) recommended deep plowing in late July and August for control of false wireworms in the Pacific Northwest.

Wade and Boving (1921) found that late fall and early spring plowing reduced populations of *Embaphion muricatum* in Kansas, while Swenk (1923) noted that plowing in May in Nebraska destroyed pupae of *Eleodes opaca.* McColloch (1918) found that 80-95% of all pupae of *E. opaca* were killed by plowing in May.

Cultural Control

The cultural controls found most effective for suppression of false wireworms consist of 3 types: summer fallow, crop rotation, and weed control. McColloch (1918) found that in nearly all cases the greatest injury by *E. opaca* occurred on land that was planted to wheat each year. Those fields that had been in a row crop or were fallowed the previous year sustained little or no damage. Systematic rotations in Kansas with such crops as sweet sorghum, kafir, milo, and (under certain conditions) corn, would reduce the populations to below economic levels. Call and Salmon (1918) suggested a rotation of wheat for 2 yr, sorghum for 1 yr, and summer fallow for 1 yr for western Kansas. This system reduced false wireworm injury and increased the yields (McColloch 1918).

During the summer months, large numbers of adults were found under Russian thistles, in clumps of volunteer grain and weeds in the fields as well as near the edges of fields (McColloch 1918, 1919, Wade and Boving 1921, Swenk 1923, Wade and St. George 1923, Wakeland 1926). Elimination of these sheltered situations by summer fallowing and by good weed control practices reduced both adults and larvae around individual fields. Summer fallowing not only controlled weeds but reduced roots and rotting vegetation, thus eliminating larval food. Frequent soil disturbances during this operation also destroyed eggs, young larvae, and pupae.

Wakeland (1926) found that summer fallowing was not effective in controlling E. hispilabris in Idaho. He suggested that the adults were mobile enough to move from hibernation sites some distance away to lay eggs in clean summer-fallowed fields. He was able to effect control by eliminating weed growth along field edges and in waste places.

Swenk (1923) found that winter wheat seeded in August and September in Nebraska sustained very heavy damage by E. opaca. Since larval activity ended in October, he recommended delaying seeding until mid-October. He noted a reduction in yield by such late seeding; however, the loss to the false wireworm larvae in wheat sown earlier exceeded this reduction in yield. Early seeded spring wheat was damaged by larvae that resumed feeding in March and April. If spring planting was delayed until May, the seeds escaped such larval damage. Late spring seeding, however, also resulted in a reduction in yield.

Chemical Control

Wade and St. George (1923) recognized that treating the seed with toxic chemicals would be much more efficient than broadcasting the chemicals. The amount of insecticide applied would also be less. They tested tar, shellac, copperas, strychnine, cyanide of potassium, turpentine, and kerosene. Many of these products significantly reduced seed germination and none were effective as killing agents. However, they did protect the seed by making it so distasteful that larvae did not feed. Broadcast treatments of crude oil or turpentine at levels necessary to kill larvae also killed vegetation. They tested poisoned bran (chemical not identified) which was successful for grasshopper control but was ineffective for false wireworm control.

Wakeland (1926) used arsenicals and Paris green in combination with moistened bran against E. hispilabris in Idaho. The poisoned mixture was applied in furrows to control adults in late summer. He found that because adults overwintered and laid eggs the following spring, intensive control of adults during the fall resulted in reduced larval populations the next spring.

Hyslop (1912) tested lead arsenate, strychnine sulphate, and coal tar as seed treatments. His results were entirely negative; all plots including the checks were equally attacked.

Swenk (1923) suggested that poisoned bran might be used to control adults of E. opaca because they seemed to eat it readily. Although he did not test this technique, he speculated that the bran would have to be applied during the latter part of July in bands around the "daytime hiding places of the beetles," broadcasted evenly over the field to be protected, or placed in furrows as recommended by Wakeland (1922, 1923).

McColloch (1918) was able to kill E. tricostata beetles readily in the laboratory with poisoned bran, but larvae were able to live for weeks on such a diet.

Wade and Boving (1921) found that small numbers of adults of *Embaphion muricatum* would feed on poisoned bran, but tests with larvae were not satisfactory.

Srivastava (1955) stated that seed treatments present an easy and safe method of placing insecticide exactly where it protects the seed and comes in contact with the target insect. He found that the best success in controlling *Eleodes suturalis* was with seed of Pawnee wheat treated with aldrin. More than 44% of the larvae were killed in laboratory tests. A treatment of 15% Lindane was not effective, but 25% Lindane resulted in some protection. Hamilton and Matteson (1966) experimented with several soil insecticides at several rates in the laboratory and found that at 2 lb/acre as a soil treatment, heptachlor, and possibly chlorfenvinphos, would control both large and small larvae. Lindane, dieldrin, aldrin, and diazinon might control small larvae only. None of the insecticides gave adequate laboratory control at rates equivalent to 1 lb/acre.

B. H. Kantack, Extension Entomologist at South Dakota State University recommended a broadcast treatment of chlordane at 4 lb actual ingredient/acre. He also recommended aldrin, dieldrin, and lindane as a seed treatment (personal communication).

CHAPTER IV

BIOLOGICAL FACTORS AFFECTING FALSE WIREWORMS

Diseases

Bacteria

Wade and St. George (1923) described reddish brown spots that appeared in the cuticle of larvae of *E. suturalis*, gradually enlarged, and usually resulted in the death of the insect. This disease appeared to be contagious. Matteson (1966) also mentioned small red spots that appeared on the cuticle of the same species, and Swenk (1923) described red spots on larvae of *E. opaca.*

I saw similar spotting on several larvae in the *E. suturalis* colony, and occasionally some larvae died because of this disease. These larvae had numerous large spots on the cuticle that spread until most of the body was reddish brown. H. C. Schroeder was able to isolate, culture, and identify the disease organism as *Serratia marscesans* Bizio, an organism that has been implicated as a disease of several other insects (Steinhaus 1949, Bucher 1963). This bacterium is also commonly found in soil (Alexander 1961). The disease appeared to be chronic when present in the culture pans and did not completely kill all of the individuals in any of the pans. Early stages of the disease were noted in field-collected larvae of *E. opaca.*

Black spots similar to the red spots were also observed several times on larvae of *E. suturalis* in the laboratory colony. Possibly these are another strain of the same disease, or certain environmental factors create a change in color of the site of infection. Black spots were noticed on larvae of E. opaca collected at various times in the field. However, the incidence of these diseased larvae never exceeded 5%.

Fungi

Wade and St. George (1923), working with E. suturalis, and Swenk (1923), working with E. opaca, implicated 2 fungi, Sporotichium globuliferum Speg. and Metarrhizium anisoplae Metschn., as diseases. I noticed growth of fungi on several dead larvae in the laboratory colonies but assumed that these were saprophytes rather than actual mortality factors. No evidence of fungi attacking larvae was observed in the field.

Gregarines

Introduction and Literature Review.--The presence of gregarines in the mid-gut of E. suturalis was noted in the laboratory but did not seem to pose a threat to the colonies. In the course of shipping several larvae to another laboratory, a significantly high mortality occurred which led us to believe that a combination of stress and the presence of gregarines contributed to the death of these insects. Therefore, an attempt was made to understand the association between this parasite and its host.

Photomicrographs and descriptions of the forms found in the mid-gut were sent to E. N. Kozloft, Associate Director at Friday Harbor Laboratories, University of Washington, for identification.

He identified the organism as belonging to the family Stylocephalidae and the genus *Stylocephalus* that is found in several species of Coleoptera. A species isolated from an unidentified *Eleodes* beetle was described by Ellis (1913) as *S. giganteus.* McColloch (1918, 1919) reported that this species infected *E. tricostata* and *E. opaca.* However, Kozloft indicated that to his knowledge no gregarine had been isolated and identified from any identified species of *Eleodes.* He could not be sure that the gregarines we observed in the several species of *Eleodes* were the same species as described by Ellis and speculated that the species observed may have been a new species. However, he couldn't be sure until living material was examined. Several larvae that were suspected of being infested were sent to him. Apparently, because of starvation during shipping and a long holding period, the larvae that were examined had lost the infection. Another shipment was sent, but, because of pressing administrative duties, he was not able to examine the larvae immediately. Finally, all correspondence ceased and no final identification was made.

The order Gregarinida is generally separated into 2 suborders: Eugregarinina and Schizogregarinina. All "nonpathogenic" gut gregarines of insects belong to Eugregarinina and are represented by families Gregarinidae, Hirmocystidae, Stylocephalidae, Actinocephalidae, and Diplocystidae (Weiser 1963).

The life cycle of species in the suborder Eugregarinina was described in detail by Steinhaus (1949). Soon after an insect ingests a spore, the digestive juices cause the spore to liberate very small falciform sporozoites. Each sporozoite enters an epithelial cell of the intestinal wall and grows, using nutrients in the cell. At that stage, it is called a trophozoite. This stage leaves the host cell while undergoing development but frequently remains attached by a special structure called an epimerite. Trophozoites that possess epimerites are called "cephalines." Eventually the trophozoite releases its hold and moves about in the lumen of the gut, at which time the epimerite is lost. The parasite is now called a sporadin or sporont. It is usually large and vermiform in this stage. Frequently these sporadins are found attached to the end of the body of other sporadins. "This tendency to associate is a characteristic for which the name Gregarina (Latin, gregarius) is derived." However, in some genera, the sporadins do not associate until just prior to cyst formation.

Encystment begins when paired sporadins form a sphere with a thick covering. The cyst leaves the body of the host along with the feces and development continues. Gametes from the 2 sporadins unite in pairs forming large numbers of zygotes. The zygotes are surrounded by a transparent membrane to form spores. The contents break up into several parts, each of which is called a sporozoite. The cysts rupture and liberate the spores that are scattered by wind and rain over foliage and soil. They are eventually ingested by a host with its food. "The life cycle is repeated: sporozoite → trophozoite → sporadin → gamete → zygote → spore → sporozoite."

Most of the true gregarines found in association with insects belong to the tribe Cephalina. Most inhabit the alimentary tract of arthropods, and for the most part are found in numerous genera of several families including Stylocephalidae (Steinhaus 1949).

These "gut gregarines" usually are not capable of causing harm to their hosts because tissue damage caused by the attachment of trophozoites to the gut wall is compensated for by normal regeneration of the gut epithelium. Real damage is caused only by those species that infect and destroy cytoplasm of the host tissue (Weiser 1963).

Most of the literature on gregarines is systematic in nature. Very little is known about their physiology and even less is known about the biological relationships between them and their hosts. Most workers consider them to be parasites that are well tolerated by their hosts. They do destroy epithelial cells and could have a weakening effect on the host; however, that could decrease general activity and reproductive powers (Steinhaus 1949).

Materials and Methods.--To determine how prevalent gregarine infections of field populations of false wireworms were throughout the summer, periodic examinations of the mid-gut of randomly selected beetles were made in 1967 and 1968. Beetles that were recovered from the state-wide distribution study were returned to the laboratory for use in biological and life cycle studies. Two species, *E. suturalis* and *E. opaca*, were regularly collected in sufficiently large numbers that random samples could be selected for gregarine examination without jeopardizing other studies.

Adults and larvae were examined for the presence of gregarines by removing the alimentary canal and opening it longitudinally. The presence and stages of gregarines observed were recorded for each insect examined. Each stage of the life cycle was observed with a binocular dissecting microscope.

Results and Discussion.--The incidence of gregarine infection from field-collected *E. suturalis* is shown in Table 29. Examinations

Table 29.--Incidence of gregarine infection from field-collected *E. suturalis* adults, 1967 and 1968.

Date	No. examined	% infection	Stages of development	
			Trophozoite	Cyst
1967				
July 1	12	25	Few(1-10)	None
July 8	13	54	Several(11-1000)	Few(1-10)
July 14	11	36	Few	None
July 27	10	20	Few	None
August 9	3	66	Few	None
1968				
June 12	10	80	Several	Few
June 19	5	60	Several	Few
June 28	7	29	Several	None
July 3	6	33	Few	None
July 12	8	13	Several	None
July 20	7	57	Several	Few
July 26	5	20	Several	None
July 31	3	66	Several	None

covered only ca. a 40-day period in 1967. Cysts were recorded from 6 of 8 adults that were infected on July 8. The trophozoites and sporonts were found in very large numbers and were of all sizes. Two gametocysts were also found in the feces of the adults. Beetles collected on other dates that year harbored no cysts and only low numbers of the free-living forms. In 1968, cysts were found in adults collected from the field on June 12 and 19 and on July 20. During the 50-day collection period, trophozoites and sporonts were found in large numbers on each collection date except July 3.

The incidence of infection of E. opaca adults is shown in Table 30. The period of examination in 1967 extended over a period of 58 days. Trophozoites and sporonts were present in large numbers

Table 30.--Incidence of gregarine infections from field-collected E. opaca adults, 1967 and 1968.

Date	No. examined	% infection	Stages of development: Trophozoite	Stages of development: Cyst
1967				
July 13	15	60	Several (11-1000)	Few (1-10)
July 27	14	29	Several	None
Aug. 9	15	93	Several	Few
Aug. 25	11	64	Several	None
Sept. 8	8	88	Several	Few
1968				
June 19	6	0		
June 28	5	0		
July 3	8	63	Few	None
July 12	20	15	Few	None

for each collection date, and cysts were observed in collections made on July 13, August 9, and September 8. The incidence and levels of infection in 1968 were low; however, the period of examination only covered 23 days. Cysts were not observed and trophozoites and sporonts were found in very low numbers.

There did not appear to be a steady increase in incidence of infection for either species of false wireworm as the summer progressed. However, the number of adults that were examined was probably too small to draw firm conclusions. In grasshoppers, the incidence of infection of gregarines characteristically increases later in the summer and fall (Steinhaus 1949). However, the life cycle of grasshoppers is usually completed from egg to adult in 1 growing season. In contrast, both *E. suturalis* and *E. opaca* overwinter as larvae. Because considerable larval feeding occurs in the fall, gregarines could be ingested in the fall and carried through the winter within their alimentary tract. The newly emerged adults would be expected to harbor large numbers of these organisms that were ingested when they were larvae. Therefore, one would not expect a gradual increase in gregarine incidence in the adult stage through the growing season.

Examination of larvae in the laboratory colonies revealed that high incidence of gregarine infections occurred in some rearing containers while in others, infections were very low or nonexistant. Pupation rates and adult emergent records did not show any effect of gregarine infection on these colonies. However, rearing was maintained under conditions optimum for rapid growth and development with as little stress as possible. In the field, where larvae are subjected to fluctuating temperature and moisture regimes, these gregarines may be a factor in growth or survival.

Parasitoids

Perilitus sp.

C. V. Riley (1892) reported that microgaster (braconid) parasites (*Perilitus* sp.) emerged from an adult *Eleodes suturalis* collected at Belvidere, Nebraska. The beetle was being held in a cigar box and the emerging larvae moved to the corners of the box where they spun cocoons for pupation. McColloch (1918) described larvae of *P. eleodis* Viereck emerging from the anal slit of adults of *E. opaca* and *E. tricostata* in August. The larvae constructed cocoons and in the process webbed particles of soil together to camouflage the cocoons. The pupation period was from 8 to 15 days, with an average of 9 days. When McColloch placed the newly emerged adults in a chamber with adults of *E. tricostata*, the beetles exhibited a "real fear" of these small wasps. The wasps would cling to the legs of the beetles and attempt to oviposit in the abdominal sutures and at the junctions of the legs and body. Oviposition occurred on several adults so that he was able to get some valuable life history information on these parasitoids. The length of the egg and larval stages totaled 10-18 days and averaged ca. 12 days. More than 120 larvae issued from a single adult. The host would live from 12 to 48 hr after the parasites emerged and would even continue to lay eggs. The rate of parasitism may have reached 50% but probably averaged ca. 5-7%.

Swenk (1923) observed *P. eleodis* emerging from *E. opaca* but did not give any details about its life history. Wade and St. George actually reared this species from E. suturalis, E. hispilabris, E. obsoleta, E. tricostata, and E. extricota, and McColloch (1919) observed additional details of emergence. Matteson (1966b) remarked that P. eleodis attacks all species of false wireworms found in South Dakota.

Sarcophaga eleodis Aldrich

Aldrich (1915) described several adult flies larvipositing on E. hispilabris, E. tricostata, and E. obsoleta in August. Flies were reared from these beetles in September. Sometimes the fly left the host at the time of death while at other times it did not leave until several weeks after the host's death.

Barber (1918) described this parasitic fly larvipositing on the posterior tip of the left wing cover in September. When the beetle moved the tip of the abdomen and exposed the anus, the larva became active and disappeared through the anus into the body. The beetle died 13 days after the larva entered it, but the larva remained within the beetle 2 additional days before emerging. The full-grown larva did not pupate until the following March 12, and the adult emerged on April 13. This species apparently overwinters in the mature larval stage entirely separate from the host.

I observed S. eleodis emerging from adults of E. suturalis that had been collected in western South Dakota, but the incidence was less than 1%. Swenk (1923) also reported this species as a parasite of E. opaca.

Walton (1917) reported and described 3 tachinid parasitoids that attacked *Eleodes* species. *Eleodiphaga caffreyi* Walton was found emerging from *Eleodes extricata* in New Mexico and from *E. obsoleta* in Arizona. *Eleodiphaga pollinosa* Walton emerged from *Eleodes hispilabris.* He also found *Biomyia eleodivora* Walton emerging from *E. tricostata.* His accounts, however, were concerned with the taxonomic descriptions of these species and did not include life history data.

I did not observe these species in South Dakota collections.

Predators

Arthropods

Wade and St. George (1923) described several insect predators of *E. suturalis.* These include 2 carabid larvae (*Calasoma* sp. and *Harpalas caliginosus* Fab.), the pavement ant (*Tetramorium caespitum* (L.)) that attacks the pupa, and an undetermined species of robber fly (*Erax*).

Several species of large carabids occur in wheat fields in western South Dakota. The larger and most voracious are *C. obsoletum* Say, *C. calidum* Fab., *Pasimachus elongatus* LeConte, and *H. calignosus.* When placed in terrariums with larvae of false wireworms, adults of these species immediately attacked and consumed them. The *Calasoma* and *Pasimachus* beetles were unusually "ferocious": many times 2 beetles contested the possession of a single larva until it was torn to pieces.

The adults were not attacked by these predaceous beetles, however. When approached by a predator, adult false wireworms would turn away and elevate their abdomen. The predators would lightly touch their antennae to the posterior portion of the abdomen and immediately retreat. These predatory beetles would not attack even though they were confined with the *Eleodes* beetles for several days without food.

Several authors (Gissler 1879, Willston 1884, Hyslop 1912, Wade 1921, Swenk 1923, Blumberg 1961, Roth and Eisner 1962) have observed the mechanism used by many tenebrionid beetles to protect themselves from predators. It consists of a "headstand" attitude whereby the caudal portion of the body is elevated. If the beetle is disturbed sufficiently, it responds by ejecting a brown liquid from the tip of its abdomen, either downward or to either side. The headstand is important because the exuded chemical then covers most of the ventral portion of the body to give maximum protection. The repelling portion of the secretion has been identified by Chadha et al. (1961) and Blumberg (1961) as simple organic compounds called quinones. I found the vapors irritating to the eyes and the liquid itself created a burning sensation when it came in contact with an open wound or a mucous membrane. The liquid also stained the skin of one's fingers a dark brown or purple color (Eisner 1966).

Willston (1884) observed *E. suturalis, E. obsoleta, E. extricata,* and *E. hispilabris* to secrete this protective substance and to assume this "headstand" attitude. He and Wade (1921) stated that *E. tricostata* did not possess defensive glands but mimicked the headstand of these other species. However, Blumberg (1961) demonstrated that *E. tricostata* does possess these glands. Swenk (1923) observed this protective technique also being employed by *E. opaca.*

Wade and Boving (1921) did not mention this means of defense in dealing with *Embaphion muricatum*; however, I have observed the headstand attitude many times with this species and have had my fingers stained by the emitted chemical.

This peculiar headstand attitude has earned this group of insects the name "circus bug." They are also referred to as "stink bugs" by several authors because of the odor of the defensive secretion.

Mammals

Predation of false wireworms by mammals was not often referred to in the literature. Wade and St. George (1923) mentioned that various species of mice may be important predators of the larvae. McColloch (1918) reported skunks eating both adults and larvae. Eisner (1966) discovered that the grasshopper mouse (*Onychomys* sp.) was able to avoid the defensive chemicals of *E. longicolbis* by pushing the abdomen of the beetle into the sand, removing the head, and devouring the internal portions. Evidence of extensive predation by this mammal was the large number of empty beetle abdomens bearing rodent tooth marks scattered throughout the desert areas of Arizona.

Birds

Wade and St. George (1923) listed the following birds as predators of false wireworms as determined by the Bureau of Biological Survey, U.S. Dept. of Agriculture: crow, hairy woodpecker, sparrow hawk, road-runner, red-headed woodpecker, sage thrasher, mockingbird, magpie, purple grackle, meadow lark, Arkansas kingbird, yellow headed blackbird, loggerhead shrike, upland plover, mallard, baldpate, burrowing owl, northern shrike, and Brewer's blackbird.

I observed lark buntings, western meadowlarks, horned larks, and dickcissels feeding in fields heavily infested with false wireworm larvae. They appeared to be digging into the soil by scratching and probing. However, I did not collect any of these birds to determine if they were actually consuming the larvae.

McColloch (1918) observed that chickens were the most efficient predator on both adults and larvae.

Wakeland (1926) had the opinion that natural enemies were of little consequence in the population dynamics of false wireworms. He also discounted the benefits of cultural control.

CHAPTER V

COLONIZATION OF FALSE WIREWORMS IN THE LABORATORY

Some aspects of most biological studies of insects are conducted in the laboratory under controlled conditions. Various stages of the insects involved are maintained and frequently reared to obtain the desired information. The ease with which the insects are maintained and the desire for large numbers of specimens frequently result in the development of a method for rearing these insects continuously. This occurred when Matteson began working with false wireworms at the Northern Grain Insects Research Laboratory in 1962. He developed a mass rearing technique for E. suturalis and suggested that this technique could be used for other false wireworm species found in South Dakota (Matteson 1966a, 1966b). These techniques, with modifications, were followed during this investigation for developing rearing procedures involving the other species.

Basic Rearing Procedures

The basic rearing procedures were similar to those developed by Matteson (1966a, 1966b); therefore, I will not repeat his detailed descriptions but will only include procedures that deviated from his.

Adults of all species were collected throughout western South Dakota by using pitfall traps as previously described. The beetles were brought to the laboratory for biological studies and for the establishment of laboratory colonies. Adults were confined to oviposition chambers, and wheat kernels were provided as food. The wheat kernels were soaked in water for 24 hr before being placed in oviposition chambers containing *E. opaca.* Eggs were collected in the manner previously described.

In an effort to increase hatchability, eggs were surface sterilized to reduce contamination. To kill organisms, especially fungi, present on the outside surface of eggs, they were soaked in sodium hypochlorite and acetic acid solutions of various concentrations for 10, 20, and 30 min. These eggs along with eggs that had not undergone such treatments were maintained on filter paper in petri dishes to determine the percent hatch. The effect of these solutions is shown in Table 31.

The hatchability of eggs was not materially affected by the treatments. However, the hatchability of those treated with acetic acid was consistently lower than the check, but the differences were not significant. Therefore, these treatments were not adopted. Control of gregarines may have resulted from the treatments, but since these organisms did not seem to adversely affect the larvae, there was probably little advantage for control of other organisms because the larvae were placed in unsterilized soil for rearing.

Newly hatched larvae were transferred to rearing pans (30X27.5X15 cm) of galvanized metal which were filled ca. 3/4 full with a moist sandy soil-vermiculite mixture. Course ground wheat was sprinkled uniformly over the surface to serve as food. About 1000-1500 larvae were maintained in each container. The containers were placed in

Table 31.--The effect of dilute sodium hypochlorite and acetic acid on the hatchability of eggs of *E. suturalis*.

Solution	Concentration	Time (min)	% hatch	Total no. eggs
Sodium hypochlorite	0.1%	10	48	150
		20	51	150
		30	46	150
	0.2%	10	80	100
		20	59	100
		30	51	100
	0.5%	10	59	100
		20	66	100
		30	44	100
Check		0	57	300
Acetic acid	0.1%	10	45	125
		20	42	125
		30	47	125
	0.2%	10	47	100
		20	23	100
		30	48	100
	0.5%	10	39	100
Check		0	50	525

a small rearing room on shelves at constant conditions of 27°C and 80-90% RH. The soil in the pans was stirred by hand frequently to determine the general condition of the larvae and the media. Some fungal growth occurred on the larvae and the media. Some fungal growth occurred on the ground wheat, thus forming a crust on the surface of the soil; however, stirring of the soil prevented this crust formation and helped to incorporate the food into the rearing media. When the soil began to feel dry, water was sprinkled over the surface to dampen it to prevent dessication of the young larvae.

After ca. 4 weeks, whole kernels of wheat were spread generously over the surface of each pan. By that time, the larvae had grown enough to eat these larger food items. However, a problem arose when the wheat germinated and grew in the pans. Such growth was prevented by placing the wheat in gallon jars in an oven for 6 hr at 80°C, thus killing the embryos.

Occasionally, mite populations built up in the soil and mites were found on the larvae in large numbers. These posed no threat to the larvae but rather indicated an untidy situation. These mites were controlled by 2 methods: the soil was treated with dicofol to which E. suturalis had a high tolerance (Hamilton and Matteson 1966), or the soil was changed in the rearing containers.

When larvae of E. suturalis and E. hispilabris reached the 10th instar, they entered a state of diapause that was only broken by exposure to temperatures near 4°C for 2 months (Matteson 1966b). Before larvae were placed in the cold room, they were removed from the rearing containers and placed in clean contrainers with fresh soil. Only 100 larvae were put in each container; when more than that were included, the mortality increased directly with the increase in larval numbers. For instance, one pan had 380+ larvae when it was placed in the cold room. Two months later, when it was examined, only 50 larvae were still alive. Only ca. 10% mortality occurred in those pans containing 100 larvae.

If the diapause could be easily broken, the rearing time for these 2 species would be reduced by ca. 25%. R. L. Gallun, Lafayette, Indiana, (personal communication) accidently discovered a method of breaking diapause in the cereal leaf beetle, *Oulema melanopus* (L.). A thermostat failure in a growth chamber containing these insects resulted in the temperature reaching near 50°C for a short period of time. The insects in the pupal stage began emerging long before expected, indicating that the high temperatures may have broken the diapause. In an attempt to break diapause in *E. suturalis* larvae, I put 100 larvae in each of 3 containers preheated to 38, 49, and 66°C for ca. 2 min. Longer exposures to these temperatures resulted in high mortality rates. Of the 100 larvae exposed to 38°, 6 developed to the prepupal stage, 4 of which became pupae, and 1 adult emerged. Of the larvae exposed to 49°, no prepupae developed. Four pupae developed from 10 prepupae and 1 adult emerged from those 100 larvae exposed to 66° temperatures. This technique did not appear to be a feasible method of improving the basic procedure; therefore, it was not incorporated into the program.

Wright (1972), working for American Cyanamid Company and maintaining a colony of false wireworms supplied by the Northern Grain Insects Research Laboratory, developed a way of circumventing the cold treatment for breaking diapause. This consisted of rearing the larvae for 2-3 weeks at 27°C, then for ca. 3 months at 22°C followed by a return to 27°C temperature for pupation which began 5 weeks later. This technique, which resulted in ca. 90% pupation, reduced the total rearing time from 6-8 months to 4 1/2-5 months. Unfortunately, I did not have the opportunity to test it with our colony.

A very small number (ca. 5%) of *E. hispilabris* larvae did not require a cold treatment before pupation. An attempt was made to select a strain that did not have a diapause; however, due to the low numbers of available larvae, we were not successful.

Other species did not have a larval diapause, and they completed their development in the same containers. Newly emerged adults were removed from the rearing containers and placed into individual holding chambers until their exoskeletons had completely hardened. They were added to the colony several days later if not used for other purposes.

Several species were successfully reared in the laboratory, but, with the exception of *E. suturalis,* none were more prolific than *Embaphion muricatum*.

The rearing of *E. muricatum* followed the techniques developed by Matteson (1966a, 1966b). However, after a period of time, modifications were made to develop a more efficient system. To develop a strain that had a faster rate of development, those adults that emerged earliest from a rearing pan were selected for a separate colony. After 3 generations, the development time of this colony was reduced to ca. 60 days from egg to adult.

Because the development time for E. muricatum was rapid and because females oviposited for a long period of time, there were always large numbers of adults available. Therefore, to reduce handling, I placed the adults directly into the larval rearing containers and allowed them to oviposit in the soil media. Because the expected egg hatch was ca. 50%, 100 females would yield ca. 1700 newly hatched larvae/week. By transferring the adults to new containers each week, the handling could be held to a minimum. These containers were kept in a rearing room that was maintained at 27° and 80-90% RH. After ca. 60 days, adults began to emerge. These were held in separate containers for ca. 7 days to allow sufficient time for their exoskeletons to harden before they were placed in the rearing program. This reduced injuries caused by contact with mature adults.

Nineteen-liter pails with metal lids were also used as rearing containers. About 11 liters of moist sandy soil mixed with vermiculite were placed in each pail. More insects could be maintained per container and special precautions did not have to be made to insure the continuation of proper humidity levels. The only maintenance required was the periodic addition of food to maintain the culture.

Adults were allowed to remain in these pails from 2 to 3 weeks, which meant that each pail probably contained ca. 5000 newly hatched larvae.

These techniques required only ca. 4 hr of technical labor each week to maintain a colony of 100,000 insects.

Dissemination of and Uses for False Wireworm Colonies

There are several advantages to having a large supply of each stage of an insect species. Many species such as house flies, cockroaches, and stored-grain insects are easily reared and have been cultured for many years. Soil insects, especially species of Coleoptera, have not been commonly reared and few physiological and biochemical experiments have been conducted on this group because of the lack of a good rearing procedure. Matteson (1966a, 1966b) listed several possible investigations that could be conducted using *E. suturalis*. These included studies involving molting or diapause hormones, sex pheromones, defensive secretions, and nutrition experiments.

His publications resulted in several requests for adults and larvae from the Northern Grain Insects Research Laboratory. These requests were forwarded to me. The following individuals and companies received insects with which to start colonies for use in their areas of interest:

Dr. C. H. Schmidt, Metabolism and Radiation Research Laboratory, USDA, ARS, Fargo, North Dakota, for use in radiation studies.

Dr. T. Eisner, Cornell University, Ithaca, New York, for work on chemical defensive secretions of adults.

Dr. M. S. Blum, then at the University of Bristol, Bristol, England, for work on chemical defensive secretions of larvae.

Dr. G. M. Happ, University of New York, University Heights, New York, for work on the mechanism of quinone production in the defensive glands.

Dr. W. S. Bowers, Physiology Pioneering Laboratory, USDA, ARS, Beltsville, Maryland, for work with ecdysone and juvenile hormone in termination of diapause.

Dr. J. W. Matteson, Monsanto Company, St. Louis, Missouri, for insecticide screening tests.

Dr. Elton E. Clark and Mr. D. P. Wright, Jr., American Cyanamid Company, Princeton, New Jersey, for insecticide screening tests.

Dr. A. E. Doty, Dow Chemical Company, Midland, Michigan, for insecticide screening tests.

Dr. R. F. Markey, Plant Protection Limited, Berkshire, England, for insecticide screening tests.

DISCUSSION AND CONCLUSIONS

False wireworms were important pests of wheat during the early part of this century, and the cropping practices of that time were synchronized with the life cycle of several species. However, a widespread change in cropping practices occurred during the 1920's and 1930's. Farmers began to alternate wheat with other crops, and they began a practice called summer fallowing in which wheat was only grown in a field in alternate years and the fields were kept free of vegetation during the other years. This practice was very detrimental to false wireworms because it broke the crop continuity necessary for the completion of their life cycles. The economic importance of false wireworms seemed to decline quite sharply, and the mention of economic infestations no longer appeared in scientific literature.

The recent occurrence of several small scattered infestations prompted another look at this group of insects to determine what potential exists for another major problem to arise. The 1st step was to determine what species occurred in South Dakota and then to survey the literature looking for clues to their life cycles. All of the life history work had been done in other states under different climatic regimes, hence it was important that this data be updated and be derived from insects that were adapted to South Dakota conditions.

False wireworms are found primarily in the semi-arid to arid portions of the United States. Crops grown under dry-land conditions include spring and winter wheat, rye, oats, barley, corn, grain and forage sorghum, and flax, all of which have some degree of susceptibility to Eleodes suturalis and Embaphion muricatum and are probably attacked by other species.

The laboratory and field life history data, when combined and interpreted, revealed which species were best adapted for damaging various crops. Their distribution in relation to field edge and topography gave insights into where localized damage may occur and what species might be involved. The distribution in relation to soil type allows one to predict which species might be important in various portions of the state.

Eleodes suturalis occurs in the active feeding stage at only one critical time period for small grain production, during the fall when winter grains are sowed. There appears to be no danger to spring seeded grains. Crops such as grain sorghum and corn which are seeded later in the spring may be susceptible to the next generation of larvae arising from overwintered adults. This species could be important in most semiarid portions of the state regardless of soil type.

Eleodes opaca larvae feed actively in both fall and spring and are potential threats to grain planted at either time. They occur quite abundantly on both clay and sandy soils which comprise most of the winter wheat belt in South Dakota. This species probably is the most economically important false wireworm in the state.

Eleodes hispilabris occurs primarily on sandy soils and seems to be a threat only to fall-seeded grains. High populations were never found in South Dakota during this study. Economic populations have been reported in Idaho and eastern Washington and only mentioned in passing by workers in the Great Plains States. The climatic conditions or the cropping sequences may be detrimental to the life cycle of this species. At any rate, it doesn't appear to be a major threat to crops in South Dakota.

Eleodes tricostata is found to inhabit grasslands more abundantly than grain fields and to occur in more humid areas than other species. McColloch (1918) indicated that larval feeding may be confined to the roots of grasses which may be why I had very little success with rearing the species on wheat kernels. To classify the potential of this species as a crop pest, a detailed study of its food habits should be conducted.

Eleodes extricata and *E. obsoleta* are found almost exclusively on sandy soils, and actively feeding larvae are found during both the fall and the spring, thus making these species threats to fall- and spring-seeded grains. Although *E. obsoleta* was captured more frequently than *E. extricata,* it never occurred in large enough numbers to attract attention in the past or during this study. Thus, the conditions necessary to cause economic problems have not been identified for either species.

All stages of *Embaphion muricatum* are present throughout most of the growing season, mostly on loam and sandy soils. The impact of the population would not be as severe because not all individuals would be in the active feeding stages simultaneously. The feeding preference studies revealed that seeds of introduced plants are attacked more readily and that most grain crops are susceptible, indicating that when populations are high enough, economic damage could occur during any part of the growing season.

False wireworms occur in low numbers in almost all wheat fields in western South Dakota. These populations are probably kept low by the practice of summer fallowing which removes food material and mechanically destroys certain stages of these insects. Because they are flightless, these insects would not be expected to reinfest fields from long distances. Although each species has one generation per year, the fecundity is high enough that, under the proper conditions, the population could increase dramatically in 1 or 2 generations. In the past, populations developed near accumulations of straw, in weedy and trashy fields and particularly in fields in which wheat was grown for 2 or more consecutive years.

Several conditions would encourage farmers to grow wheat continuously. Higher yields could result from (1) a drought resistant wheat which would produce high yields with less rainfall than current varieties and (2) occurrence of rain in the early fall which would indicate to farmers that there is sufficient moisture to establish a stand and the normal spring rains would carry the crop through to harvest. Also, seeding in stubble may be a technique whereby a farmer might gamble that enough snow will be trapped and enough moisture would be available to create a good yield. In addition, other factors influencing continuous wheat would include (1) land prices and taxes high enough to convince farmers that they could not afford to let their land lie idle every other year, (2) the price of wheat increased to the point that even a nominal yield would be profitable to harvest, and (3) relaxation of wheat acreage allotments. These factors would probably work in combination. Moisture availability would be the primary factor that farmers would use to decide whether it was practical to plant wheat continuously in a field. These other factors would either lower the minimum moisture threshold or would determine how willingly a grower would gamble on the outcome.

There is evidence that some farmers are now beginning to grow wheat continuously near Quinn and Elm Springs, South Dakota (P. A. Jones, Survey Entomologist, S. D. State University, personal communication). Apparently, by applying liquid nitrogen and seeding in the stubble, yields were only reduced by 20%. Because the price of wheat has risen so sharply in 1973, even low yields of wheat became profitable to harvest. High prices will probably encourage still more farmers to grow wheat for consecutive years in the same fields.

When wheat is sown in the fall with sufficient moisture available, germination occurs quite rapidly, and even though moderate populations of false wireworms might be present, most of the wheat would escape damage. If wheat was sown in the same field the following year, the population level would probably be higher, and even though sufficient moisture might be available for rapid germination, some damage would probably occur. More importantly, the populations would increase each year that wheat was grown continuously until an economic threshold would be reached. That threshold would depend both on the population level and on the amount of moisture available at seeding time. The amount of available moisture, if limited, would directly affect the speed of germination and would determine the length of time the plant would remain in the susceptible seed and young seedling stage.

The possibility of false wireworms becoming economically important after more than 40 years is not just idle speculation. B. J. Kantack (Extension Entomologist, S. D. State University) and P. A. Jones (personal communication) reported that over 5,000 acres of wheat were destroyed by false wireworms in eastern Pennington Co. in 1973. During the previous 10 years, the only false wireworm damage in South Dakota was reported by the author. Usually these widely scattered infestations were discovered in the course of conducting this study. It is interesting to note that the widespread damage by these insects is occurring in the same general area where wheat is being grown continuously. As this practice spreads, the insect problem will probably also increase. In the not too distant future, false wireworms may again be the limiting factor in the growth of dryland wheat on the Great Plains.

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ADDENDUM I

Pitfall trap locations in South Dakota - 1964 to 1968.

1964

1. Bon Homme Co. - 2.3 miles W of junction highways 37 and 50, oat field, level, silty clay loam, June 10 to August 5.

2. Gregory Co. - 4.5 miles W of Burke, S side of winter wheat field, top of slope, silt loam, June 10 to August 5.

3. Tripp Co. - 4.6 miles W of Dallas, S edge of winter wheat field, top of rise, level, clay, June 10 to August 5.

4. Bennett Co. - 6.1 miles W of Vetal, S edge of winter wheat field, level, sandy loam, June 10 to August 5.

5. Bennett Co. - 11.7 miles W of Vetal, S edge of winter wheat field, level, sandy loam, June 10 to August 5.

6. Bennett Co. - 2.1 miles W of Swett, S edge of winter wheat field, level, sandy loam, June 10 to August 5.

7. Shannon Co. - 2.6 miles E of Pine Ridge, S side of oat field, level, light loam, June 10 to August 5.

8. Custer Co. - 21.7 miles N of junction of highways 79 and 18, E edge of oat field, level, clay loam (not as according to soil map) June 10 to August 5.

9. Pennington Co. - 2.6 miles E of Ellsworth Air Force Base Main Entrance, N side of winter wheat field, level, clay, June 10 to August 5.

10. Pennington Co. - 5.2 miles E of New Underwood, N side of winter wheat field, level, clay, June 10 to August 5.

11. Pennington Co. - 2.1 miles E of junction of highways 14 and 16 on highway 14, S edge of winter wheat field, 10% slope to the E, silty clay loam, June 10 to August 5.

12. Jackson Co. - 3.3 miles E of Cottonwood, S edge of winter wheat field, level, clay, June 10 to August 5.

13. Haakon Co. - 13.4 miles E of Philip, S side of winter wheat field, level, clay, June 10 to August 5.

14. Stanley Co. - 9.4 miles N of Midland, E edge of winter wheat field, level, clay, June 10 to August 5.

15. Stanley Co. - 2.5 miles E of Hayes, S edge of winter wheat field, level, clay, June 10 to October 31.

16. Stanley Co. - 11.0 miles E of Hayes, S side of winter wheat field, level, clay, June 10 to October 31.

17. Haakon Co. - 25.5 miles W of junction of highways 34 and 14 on highway 34, N edge of winter wheat field, level, clay, August 27 to September 10.

18. Ziebach Co. - 26.6 miles W of Billsburg, S side of winter wheat field, level, clay, September 10 to October 31.

19. Meade Co. - 3.7 miles W of Howes, S side of winter wheat field, slight W slope, clay, September 10 to October 31.

20. Meade Co. - 3.1 miles W of White Owl, N side of winter wheat field, level, sandy loam, September 10 to October 31.

21. Meade Co. - 23.8 miles W of Union Center, just W of Belle Fourche River, S edge of spring wheat field, E slope, clay, September 10 to October 31.

22. Meade Co. - 5.2 miles W of Bear Butte, S side of winter wheat field, level, clay, September 10 to October 31.

23. Lawrence Co. - 1.0 miles W of St. Onge, NE edge of winter wheat field, level, clay, September 10 to October 31.

24. Harding Co. - 3.6 miles NE of Buffalo, E side of oat field, top of gentle rise, sandy loam, September 10 to October 31.

25. Harding Co. - 2.1 miles N of Ludlow, W side of spring wheat field, level, loam, September 10 to October 31.

26. Harding Co. - 0.1 miles E of Reva, S side of spring wheat field, level, loam, September 10 to October 31.

27. Perkins Co. - 11.1 miles E of Bison, N edge of spring wheat field, level, loam, September 10 to October 31.

28. Meade Co. - 0.2 miles N of junction of highways 212 and 73, W edge of spring wheat field, level, sandy loam, September 10 to October 31.

29. Ziebach Co. - 2.4 miles E of Red Elm, S side of spring wheat field, level, sandy loam, September 10 to October 31.

1965

1. Todd Co. - 3.8 miles W of Mission, S side of native grass pasture, top of slope, silt loams, April 15 to July 19.

2. Bennett Co. - 6.1 miles W of Vetal, S side of winter wheat field, level, loam, April 15 to July 19.

3. Bennett Co. - 11.7 miles W of Vetal, S side of winter wheat field, top of gentle rise, sandy loam, April 15 to July 19.

4. Bennett Co. - 3.4 miles W of Martin, S side of winter wheat field, level, sandy loam, April 15 to July 19.

5. Bennett Co. - 2.4 miles W of Swett, S side of winter wheat field, level, sandy loam, April 15 to July 19.

6. Custer Co. - 8.8 miles N of junction of highways 18 and 79, E edge of winter wheat field, slight N slope, clay loam, April 15 to July 19.

7. Custer Co. - 21.7 miles N of junction of highways 18 and 79, E edge of oat field, level, clay loam (not as according to soil map) April 15 to July 19.

8. Pennington Co. - 2.4 miles E of Ellsworth Air Force Base Main Entrance, N edge of winter wheat field, level, clay, April 16 to July 20.

9. Jackson Co. - 3.1 miles E of Cottonwood, S side of winter wheat field, level, clay, April 16 to July 20.

10. Haakon Co. - 13.6 miles E of Philip, S side of winter wheat field, level, clay, April 16 to July 20.

11. Stanley Co. - 10.0 miles N of Midland, E side of winter wheat field, level, clay, April 16 to July 20.

12. Stanley Co. - 27.7 miles E of Hayes, SE side of winter wheat field, along fence, W slope, clay, April 16 to September 30.

13. Stanley Co. - 2.5 miles E of Hayes, S edge of winter wheat field, level, clay, April 16 to September 2.

14. Haakon Co. - 11.6 miles W of junction of highways 34 and 14, N side of winter wheat field, level, clay, July 25 to August 8.

15. Ziebach Co. - 27.0 miles W of Billsburg, S side of winter wheat field, level, clay, July 25 to September 30.

16. Meade Co. - 3.7 miles W of Howes, S side of winter wheat field, slight W slope, clay, July 25 to September 2.

17. Meade Co. - 0.9 miles W of White Owl, N side of winter wheat field, level at top of gentle rise, sandy loam, July 25 to September 30.

18. Meade Co. - 23.8 miles W of Union Center, just W of Belle Fourche River, S edge of spring wheat field, slight E slope, clay, July 25 to September 2.

19. Meade Co. - 5.2 miles W of Bear Butte, S side of winter wheat field, level, clay, July 25 to September 30.

20. Lawrence Co. - 1.1 miles NW of St. Onge, NE edge of winter wheat field, level, clay, July 25 to September 2.

21. Lawrence Co. - 4.0 miles NW, 1/2 mile NE of Spearfish (Carlson's Farm), grass, level, loam, July 25 to September 2.

22. Harding Co. - 3.6 miles N of Buffalo, E side of oat field, top of gentle rise, sandy loam, July 25 to September 30.

23. Harding Co. - 0.2 miles E of Reva, S side of spring wheat field, level, loam, July 25 to September 2.

24. Meade Co. - 34.3 miles S of junction of highways 20 and 73 or 3.7 miles W of Faith, W side of spring wheat field, level, sandy loam, July 25 to September 2.

25. Ziebach Co. - 2.5 miles E of Red Elm, S side of spring wheat field, level, sandy loam, July 25 to September 2.

26. Dewey Co. - 5.6 miles E of Lantry, S side of spring wheat field, top of gentle rise, loam, July 25 to September 2.

27. Dewey Co. - 3.4 miles E of Eagle Butte, S side of spring wheat field, level with slight E slope, silty clay loam, July 25 to September 2.

1966

1. Lyman Co. - 6.8 miles W of Kennebec, N edge of oat field, E-NE slope, clay, June 2 to July 20.

2. Lyman Co. - 5.5 miles S of junction of highways 16 and 183, SE corner of winter wheat field, slight E slope, clay, June 2 to August 3.

3. Tripp Co. - 0.6 miles S of Witten Corner on highway 183, SE corner of winter wheat field, level, clay, June 2 to August 3.

4. Todd Co. - 1.4 miles W of Carter on highway 18, S side of winter wheat field, level, clay, June 2 to July 20.

5. Bennett Co. - 0.3 miles W of Vetal, S edge of winter rye field, level, sandy loam, May 18 to August 3.

6. Bennett Co. - 11.6 miles W of Vetal, S edge of winter wheat field, level, sandy loam, May 18 to July 6.

7. Bennett Co. - 2.1 miles W of Swett, S edge of winter wheat field, level, sandy loam, June 2 to August 3.

8. Pennington Co. - 0.5 miles E of County Road 473 E of Rapid City on highway I-90, NW corner of winter wheat field, level with slight NW exposure, clay, May 19 to August 3.

9. Pennington Co. - 2.1 miles E of junction of highways 16 and 14 E of Wall, S edge of winter wheat field, 10% slope to the E, silty clay loam, May 19 to August 4.

10. Jackson Co. - 3.3 miles E of Cottonwood, S edge of winter wheat field, level, clay, June 3 to August 4.

11. Stanley Co. - 9.4 miles N of Midland, spring wheat, W-SW slope 5%, clay, May 19 to August 4.

12. Stanley Co. - 4.0 miles W of Ft. Pierre, S edge of winter wheat field, level, clay, July 26 to August 9.

13. Stanley Co. - 2.1 miles E and 0.2 miles S of Hayes, W side of winter wheat field, crest of broad hill, clay, June 3 to July 21.

14. Stanley Co. - 3.1 miles E of Hayes, S edge of winter wheat field, level, clay, June 3 to July 21.

15. Stanley Co. - 0.6 miles W of junction of highways 63 and 34, NW corner of winter wheat field, level, clay, August 8 to September 21.

16. Haakon Co. - 1.4 miles W of Billsburg, S side of winter wheat field, level, clay, August 8 to September 21.

17. Meade Co. - 3.7 miles W of Howes, trashy fallow - winter wheat last year, 5° E slope, clay, August 8 to August 22.

18. Meade Co. - 6.5 miles W of Plainview, NW corner of winter wheat field, level, loam, August 8 to September 21.

19. Meade Co. - 3.1 miles W of White Owl, NW corner of spring wheat, level, sandy loam, August 23 to September 21.

20. Meade Co. - 4.8 miles W of Enning, winter wheat field - N side, level, crest of gentle rise, sandy loam, August 8 to September 21.

21. Meade Co. - 5.5 miles W of Bear Butte, S side of winter wheat field, level, clay, August 8 to September 21.

22. Harding Co. - 3.8 miles N of Buffalo on old highway, E side of oat field, top of gentle rise, sandy loam, August 9 to September 21.

23. Perkins Co. - 3.7 miles E of Prairie City, N edge of spring wheat field, level, loam, August 9 to September 21.

24. Perkins Co. - 3.4 miles E of Bison, NW corner of winter wheat field, level, loam, August 9 to September 21.

25. Corson Co. - 1.5 miles E of Keldron, N side of spring wheat field, E slope, loam, August 9 to September 7.

26. Corson Co. - 0.9 miles S of McLaughlin, SW corner of winter wheat field, gentle NE slope, loam, August 9 to September 21.

27. Corson Co. - 8.0 miles SE of McLaughlin, winter wheat field, level, rocky sandy soil (sandy loam), August 9 to September 21.

28. Walworth Co. - 5.1 miles SE of Selby, N side of spring wheat field, level, silt loam, August 9 to August 23.

29. Hughes Co. - 2.0 miles W of Blunt, NW corner of winter wheat field, level, loam soil, June 3 to September 21.

30. Hand Co. - 2.3 miles W of Vayland, S side of winter rye field, level, silt loam, June 3 to September 21.

31. Day Co. - 3.2 miles W of Webster, S side of oat field, level, silt, August 2 to September 1.

32. Day Co. - 2.2 miles N of County Line on highway 25, SW corner of oat field, level, silt, August 2 to September 1.

33. Clark Co. - 7.0 miles E of Clark, SW corner of rye field, level, silt, August 2 to September 1.

34. Spink Co. - 2.5 miles E of Doland, S side of oat field, level, clay loam, June 13 to August 16.

35. Spink Co. - 2.7 miles S of Redfield, W side of oat field, top of gentle knoll, sandy loam, June 13 to August 16.

36. Spink Co. - 4.6 miles S of Tulare, SE end of oat field, gentle N slope, sandy loam, June 13 to September 1.

37. Beadle Co. - 0.5 miles E of junction of highways 281 and 28, N side of oat field, level, sandy loam, June 22 to July 6.

38. Beadle Co. - 5.4 miles W of Cavour, S side of oat field, level, loam, June 13 to August 9.

39. Sanborn Co. - 14.0 miles S of Huron, E side of oat field, level, sandy loam, June 13 to July 28.

40. Hamlin Co. - E side of Dry Lake, N edge of oat field, level, loam, May 27 to August 24.

41. Hamlin Co. - 5 miles W and 0.5 miles S of Estelline, W edge of rye field, top of gentle rise, silt, July 1 to August 24.

42. Brookings Co. - Oakwood Lakes State Park, W edge of oat field, 5% slope to E, silt, July 18 to August 24.

43. Brookings Co. - 0.5 miles W of NW corner of Goldsmith Lake, S side of oat field, top of gentle rise, silt, July 1 to August 24.

1967

1. Jerauld Co. - 6.0 miles W of Wessington Springs, SW corner of winter wheat field, level, silty clay loam, June 1 to August 7.

2. Buffalo Co. - 2.7 miles W of junction of highways 45 and 34, S side of oat field, level, silty clay loam, June 1 to August 7.

3. Lyman Co. - 8.0 miles W of Reliance, NW side of winter wheat field, level with slight N slope, clay, June 1 to September 7.

4. Lyman Co. - 3.7 miles W of Kennebec, S side of winter wheat field, level, clay, June 1 to August 23.

5. Lyman Co. - 9.5 miles S of junction of highways 183 and 16, E edge of winter wheat field, level, clay, June 1 to July 25.

6. Tripp Co. - 0.8 miles S of Witten Corner on highway 183, E end of winter wheat field, gentle N slope, clay, June 7 to August 23.

7. Tripp Co. - 6.0 miles W of junction of highways 183 and 18, winter wheat field, level, clay, June 15 to July 25.

8. Bennett Co. - 6.1 miles W of Vetal, SE corner of winter wheat field, level, loam, June 1 to July 25.

9. Bennett Co. - 7.1 miles W of junction of highways 73 and 18, S edge of winter wheat field, level, sandy loam, June 1 to July 25.

10. Bennett Co. - 3.7 miles W of Martin, S side of winter wheat field, level, sandy loam, June 7 to July 25.

11. Jackson Co. - 11.2 miles E of Kadoka, spring wheat field, top of gentle rise, clay, June 2 to July 26.

12. Stanley Co. - 10.7 miles N of Midland, E side of winter wheat field, level, clay, June 2 to July 26.

13. Stanley Co. - 1.3 miles E of Hayes, N side of winter wheat field, level, clay, June 16 to July 26.

14. Haakon Co. - 0.6 miles W of junction of highways 63 and 34, N side of winter wheat field, level, clay, June 8 to July 26.

15. Haakon Co. - 12.2 miles W of junction of highways 63 and 34, N side of winter wheat field, level, clay, August 10 to August 24.

16. Haakon Co. - 5.4 miles W of Billsburg, S side of winter wheat field, level, clay, June 8 to July 26.

17. Meade Co. - 3.3 miles W of Faith, W side of spring wheat field, level, sandy loam, June 8 to June 30.

18. Perkins Co. - 3.5 miles N of Usta, W side of spring wheat field, level (low), loam, June 8 to August 8.

19. Perkins Co. - 4.0 miles E of the S junction of highways 20 and 73, S side of spring wheat field, level, loam, June 8 to August 8.

20. Ziebach Co. - 7.3 miles E of Glad Valley, SW side of oats field, level, loam, June 8 to August 24.

21. Dewey Co. - 1.2 miles E of S junction of highways 65 and 20, S side of winter wheat, level, sandy loam, June 8 to August 24.

22. Dewey Co. - 0.4 miles E of Isabel, N side of oat field, level, sandy loam, June 8 to July 27.

23. Dewey Co. - 4.2 miles E of Timberlake, N side of oat field, level, sandy loam, June 8 to July 27.

24. Dewey Co. - 3.9 miles E of Trail City, N side of spring wheat field, level, loam, June 23 to July 27.

25. Walworth Co. - 7.7 miles E of Glenham, N side of spring wheat field, level, sandy loam, June 8 to July 27.

26. Walworth Co. - 2.7 miles E of S junction of highways 12 and 83, S side of spring wheat field, level, loam, June 8 to September 7.

27. Potter Co. - 5.4 miles S of Hoven, E side of spring wheat field, level, sandy loam, June 8 to September 7.

28. Potter Co. - 2.0 miles E of N junction of highways 47 and 212, S side of spring wheat field, level, loam, June 2 to September 7.

29. Faulk Co. - 6.5 miles E of Seneca, N side of spring wheat field, level, loam, June 2 to August 9.

30. Faulk Co. - 4.1 miles E of Faulkton, E side of spring wheat field, level, loam, June 24 to July 27.

31. Spink Co. - 2.9 miles S of Redfield, W side of oat field, top of gentle knoll, sandy loam, June 2 to August 9.

32. Spink Co. - 4.6 miles S of Tulare, SE end of oat field, gentle N slope, sandy loam, June 2 to August 9.

1968

1. Jerauld Co. - 8.5 miles W of Wessington Springs, SW corner of wheat field, level near top of hill, loam, May 7 to August 5.

2. Buffalo Co. - 5.0 miles W of junction of highways 45 and 34, SW corner of wheat field, level, loam, May 7 to July 18.

3. Lyman Co. - 1.2 miles W of Lyman, NW corner of oat field, level - slight slope to NE, clay, May 7 to July 26.

4. Lyman Co. - 1.3 miles W of Kennebec, winter wheat field - S side, level, clay, May 7 to July 24.

5. Lyman Co. - 7.6 miles S of junction of highways 183 and 16, E side of winter wheat field, level, clay, May 7 to July 24.

6. Tripp Co. - 0.7 miles S of Ideal corner on highway 183, E side of winter wheat field, gentle S-facing slope, clay, May 7 to July 24.

7. Tripp Co. - 6.6 miles W of junction of highways 18 and 183, W side of winter wheat field, level, clay, May 7 to July 24.

8. Bennett Co. - 5.2 miles W of Vetal on U.S. Highway 18, S side of winter wheat field, level, sandy loam, May 7 to July 24.

9. Bennett Co. - 3.7 miles W of junction of highways 18 and 79, S side of winter wheat field, top of a gentle rise, sandy loam, May 7 to July 24.

10. Bennett Co. - 7.3 miles W of Martin, S side of winter wheat field, near top of a gentle rise, sandy loam, May 7 to July 24.

11. Jackson Co. - 11.5 miles E of Kadoka, spring wheat field, slight slope near top of hill, clay, May 13 to July 24.

12. Jackson Co. - 1.5 miles N of junction of highways 16 and 73, W side of winter wheat field, level, clay, May 13 to July 24.

13. Jones Co. - 2.0 miles E of Okaton, winter wheat field, S side at top of hill, clay, May 21 to July 10.

14. Haakon Co. - 19.8 miles N of Philip, E side of winter wheat field, top of gentle rise, clay, May 14 to July 30.

15. Haakon Co. - 3.4 miles W of Billsburg, N side of a winter wheat field, level, clay, May 14 to July 30.

16. Ziebach Co. - 0.8 miles E of Red Elm, S side of spring wheat field, level, sandy loam, May 14 to July 30.

17. Ziebach Co. - 4.6 miles N of junction of highways 212 and 65, W side of spring wheat field, gentle slope to W, loam, May 14 to July 30.

18. Dewey Co. - 1.2 miles E of S junction of highways 20 and 65, S side of oat field, level, sandy loam, May 14 to August 8.

19. Dewey Co. - 4.2 miles E of Timberlake, S side of spring wheat field, level, sandy loam, May 14 to August 8.

20. Dewey Co. - 3.9 miles E of Trail City, N side of spring wheat field, level, loam, May 14 to August 8.

21. Walworth Co. - 6.6 miles E of Mobridge, N side of spring wheat field, level, loam, May 15 to August 8.

22. Walworth Co. - 6.6 miles E of Glenham, NE corner of spring wheat field, level, sandy loam, May 23 to July 26.

23. Walworth Co. - 2.0 miles S of Selby - 200 yards off highway, S side of spring wheat field, level, loam, May 23 to August 8.

24. Walworth Co. - 10.5 miles S of junction of highways 12 and 47, W side of oat field, gentle slope to W, sandy loam, May 23 to August 8.

25. Faulk Co. - 10.5 miles E of junction of highways 212 and 47, S side of spring wheat field, level, loam, May 23 to August 8.

26. Faulk Co. - 3.0 miles E of Seneca, N side of winter rye stubble from last year, level, loam, May 23 to July 26.

27. Faulk Co. - 5.6 miles E of Faulkton, E side of spring wheat field, level, loam, May 23 to July 31.

28. Hand Co. - 2.8 miles E of Rockham, N side of spring wheat field, level, loam, May 23 to July 26.

29. Spink Co. - 2.9 miles S of Redfield, W side of spring wheat field, gentle E slope, sandy loam, May 23 to August 8.

30. Spink Co. - 4.6 miles S of Tulare, S end of oat field, gentle N slope, sandy loam, May 23 to August 8.

31. Beadle Co. - 0.8 miles E of junction of highways 37 and 28, N side of spring wheat, level, loam, May 23 to July 26.

ADDENDUM II

Distribution of Eleodes suturalis and E. opaca in the United States.

ELEODES SUTURALIS

ELEODES OPACA

Distribution of *E. hispilabris* and *E. tricostata* in the United States.

ELEODES HISPILABRIS

ELEODES TRICOSTATA

Distribution of *E. extricata* and *E. obsoleta* in the United States.

ELEODES EXTRICATA

ELEODES OBSOLETA

Distribution of *Embaphion muricatum* and *Glyptasida sordida* in the United States.

EMBAPHION MURICATUM

GLYPTASIDA SORDIDA

Distribution of *Asidopsis opaca* and *A. polita* in the United States.

ASIDOPSIS OPACA

ASIDOPSIS POLITA

ADDENDUM III

COUNTY DISTRIBUTION OF FALSE WIREWORMS IN THE GREAT PLAINS

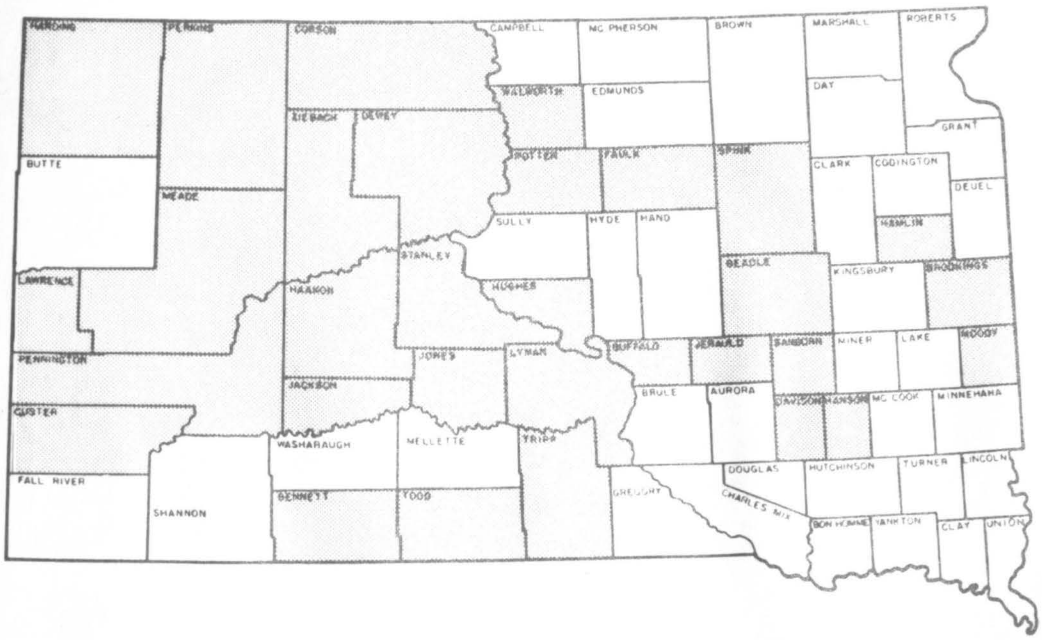
Distribution of *E. suturalis* in South Dakota and Nebraska.

South Dakota Counties

Beadle	Faulk	Jones	Sanborn
Bennett	Haakon	Lawrence	Spink
Brookings	Hamlin	Lyman	Stanley
Buffalo	Hanson	Meade	Todd
Corson	Harding	Moody	Tripp
Custer	Hughes	Pennington	Walworth
Davison	Jackson	Perkins	Ziebach
Dewey	Jerauld	Potter	

Nebraska Counties

Adams	Dodge	Hall	Scotts Bluff
Banner	Dundy	Harlan	Sioux
Box Butte	Fillmore	Jefferson	Thayer
Clay	Franklin	Lancaster	Thomas
Dawes	Furnas	Phelps	York
Dixon	Gosper	Saunders	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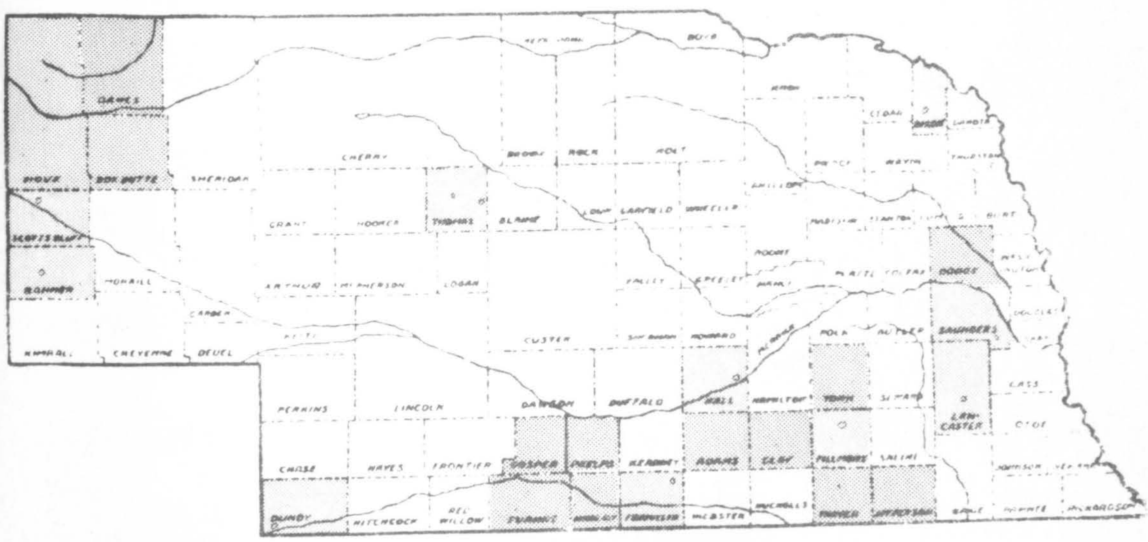
PERKINS
CORSON
CAMPBELL
MC PHERSON
BROWN
MARSHALL
ROBERTS
WALWORTH
EDMUNDS
DAY
ZIEBACH
DEWEY
GRANT
BUTTE
POTTER
FAULK
SPINK
CLARK
CODINGTON
MEADE
DEUEL
SULLY
HYDE
HAND
HAMLIN
STANLEY
LAWRENCE
HUGHES
BEADLE
KINGSBURY
BROOKINGS
HAAKON
BUFFALO
JERAULD
SANBORN
MINER
LAKE
MOODY
JONES
LYMAN
PENNINGTON
JACKSON
BRULE
AURORA
DAVISON
HANSON
MC COOK
MINNEHAHA
CUSTER
WASHABAUGH
MELLETTE
TRIPP
DOUGLAS
HUTCHINSON
TURNER
LINCOLN
FALL RIVER
BENNETT
TODD
GREGORY
CHARLES MIX
SHANNON
BON HOMME
YANKTON
CLAY
UNION



Distribution of *E. suturalis* in Wyoming, Colorado, Kansas, and Oklahoma.

Iowa County

Lyon

Wyoming County

Natrona

Colorado Counties

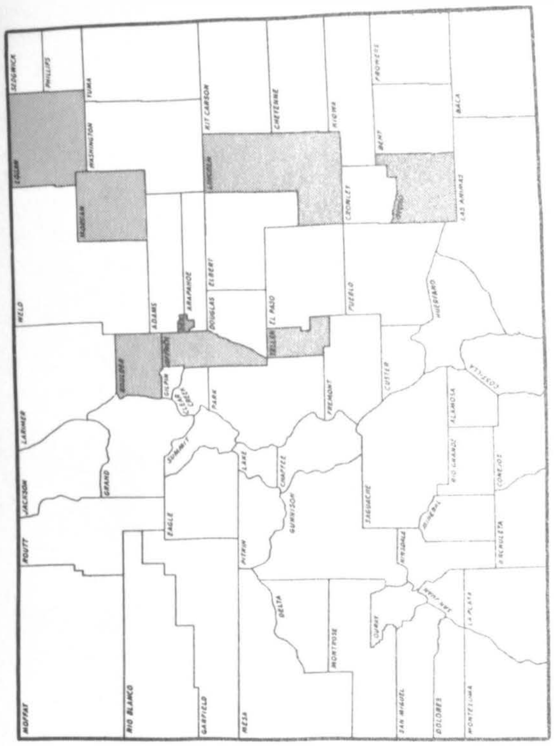
Boulder	Jefferson	Logan	Otero
Denver	Lincoln	Morgan	Teller

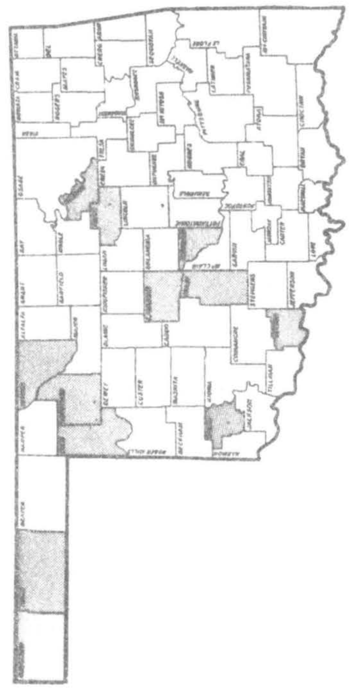
Kansas Counties

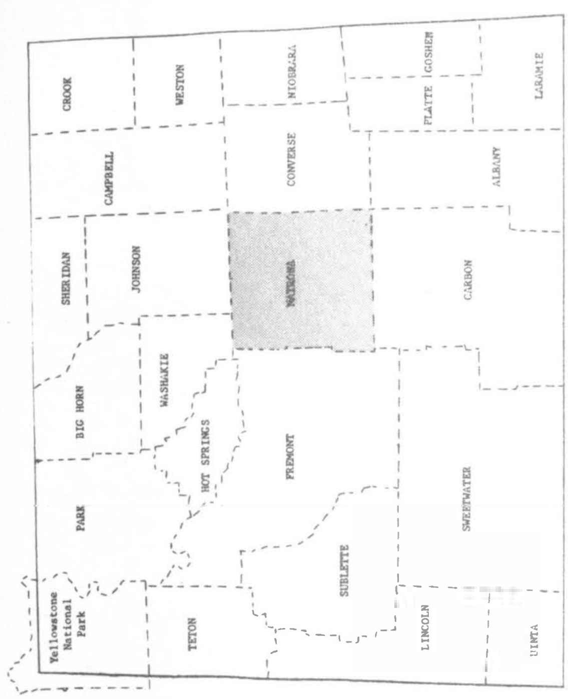
Butler	Gove	Meade	Saline
Cheyenne	Gray	Morton	Scott
Cowley	Greeley	Norton	Sedgwick
Decatur	Hamilton	Pawnee	Seward
Edwards	Harper	Pottawatomie	Sheridan
Ellis	Kingman	Pratt	Sumner
Ellsworth	Logan	Rawlins	Thomas
Finney	Marshall	Republic	Wabaunsee
Ford	McPherson	Riley	Wallace

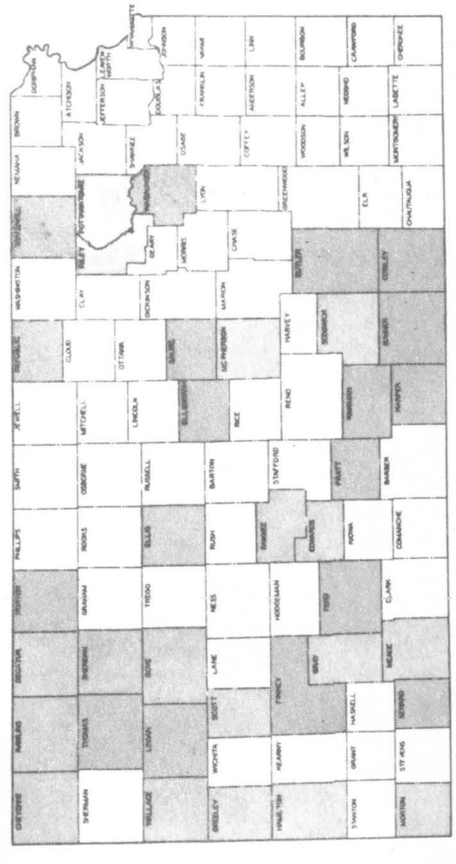
Oklahoma Counties

Canadian	Cotton	Greer	Texas
Cimarron	Ellis	Pawnee	Woods
Cleveland	Grady	Payne	Woodward






CROOK
WESTON
NIOBRARA
GOSHEN
PLATTE
LARAMIE
CAMPBELL
CONVERSE
ALBANY
SHERIDAN
JOHNSON
NATRONA
CARBON
BIG HORN
WASHAKIE
HOT SPRINGS
FREMONT
PARK
SWEETWATER
Yellowstone National Park
TETON
SUBLETTE
LINCOLN
UINTA



Distribution of *E. opaca* in North Dakota, South Dakota, Nebraska, and Kansas.

North Dakota Counties

Richland	Williams

South Dakota Counties

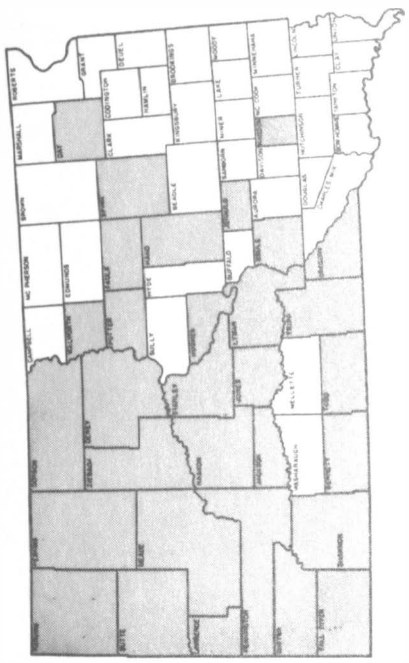
Bennett	Faulk	Jerauld	Shannon
Brule	Gregory	Jones	Spink
Butte	Haakon	Lawrence	Stanley
Corson	Hand	Lyman	Todd
Custer	Hanson	Meade	Tripp
Day	Harding	Pennington	Walworth
Dewey	Hughes	Perkins	Ziebach
Fall River	Jackson	Potter	

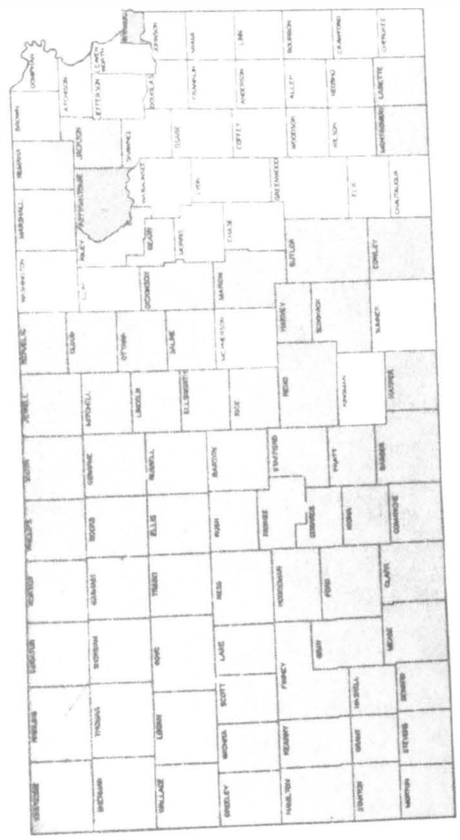
Nebraska Counties

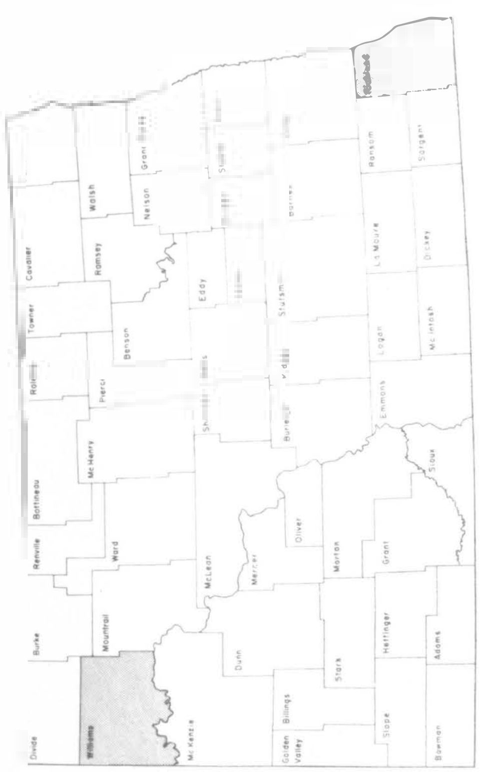
Banner	Dodge	Hayes	Nance
Box Butte	Dundy	Hitchcock	Perkins
Buffalo	Fillmore	Kearney	Red Willow
Chase	Franklin	Keith	Saline
Cheyenne	Frontier	Keya Paha	Saunders
Cuming	Furnas	Kimball	Scotts Bluff
Custer	Gage	Lancaster	Sheridan
Dawes	Garden	Lincoln	Sherman
Deuel	Harlan	Madison	Sioux
Dixon			

Kansas Counties

Barber	Grant	Meade	Rooks
Barton	Gray	Mitchell	Rush
Butler	Greeley	Montgomery	Russell
Cheyenne	Hamilton	Morton	Saline
Clark	Harper	Nemaha	Scott
Cloud	Harvey	Ness	Sedgwick
Comanche	Haskell	Norton	Seward
Cowley	Hodgeman	Osborne	Sheridan
Decatur	Jackson	Ottawa	Sherman
Dickinson	Jewell	Pawnee	Smith
Edwards	Kearny	Phillips	Stafford
Ellis	Kiowa	Pottawanomie	Stanton
Ellsworth	Labette	Pratt	Stevens
Finney	Lane	Rawlins	Thomas
Ford	Lincoln	Reno	Trego
Geary	Logan	Republic	Wallace
Gove	Marion	Rice	Wichita
Graham	Marshall	Riley	Wyandotte



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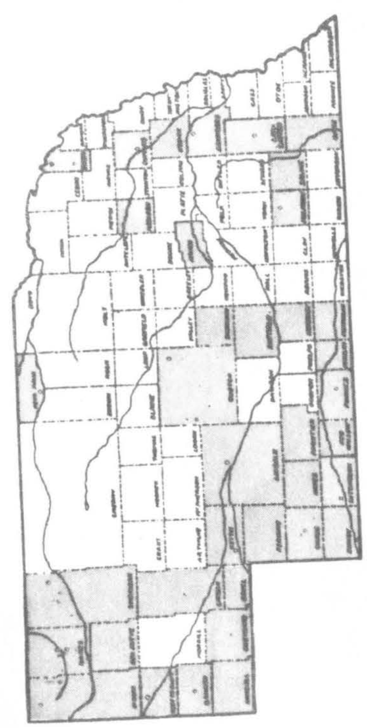
Burke
Renville
Bottineau
Towner
Cavalier
Walsh
Ramsey
Nelson
Grand Forks
Benson
Eddy
Pierce
McHenry
Ward
Mountrail
Williams
McKenzie
Dunn
McLean
Mercer
Oliver
Burleigh
Kidder
Stutsman
Logan
La Moure
Ransom
Sargent
Dickey
McIntosh
Emmons
Sioux
Morton
Grant
Hettinger
Adams
Bowman
Slope
Stark
Billings
Golden Valley



Distribution of _E. opaca_ in Montana, Colorado, and Oklahoma.

Montana County

Roosevelt

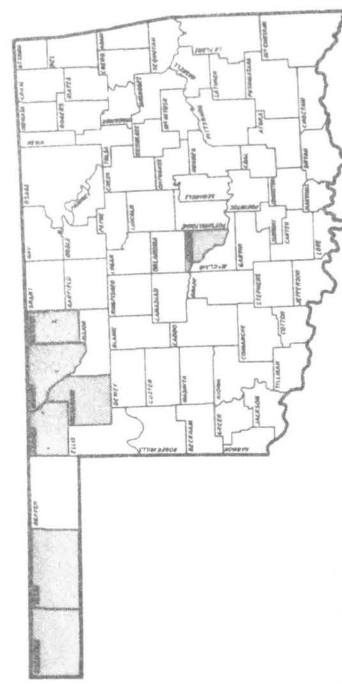
Colorado Counties

El Paso	Las Animas	Logan

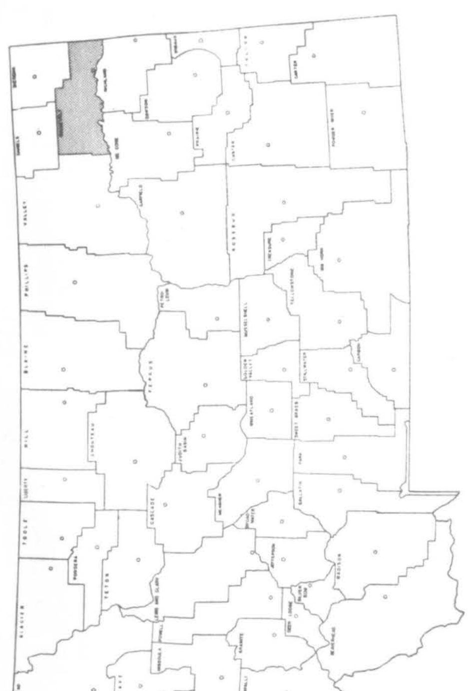
Oklahoma Counties

Alfalfa	Cleveland	Texas	Woodward
Cimarron	Harper	Woods	

COLORADO



OKLAHOMA



MONTANA

Distribution of *E. hispilabris* in North Dakota, South Dakota, Nebraska, and Kansas.

North Dakota Counties

Slope	Williams

South Dakota Counties

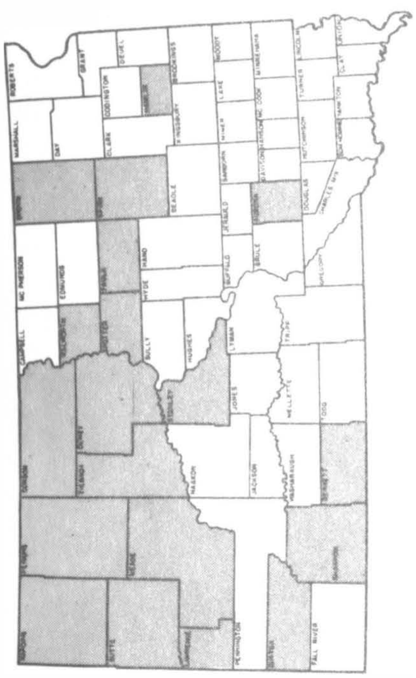
Aurora	Custer	Lawrence	Spink
Bennett	Dewey	Meade	Stanley
Brown	Faulk	Perkins	Walworth
Butte	Hamlin	Potter	Ziebach
Corson	Harding	Shannon	

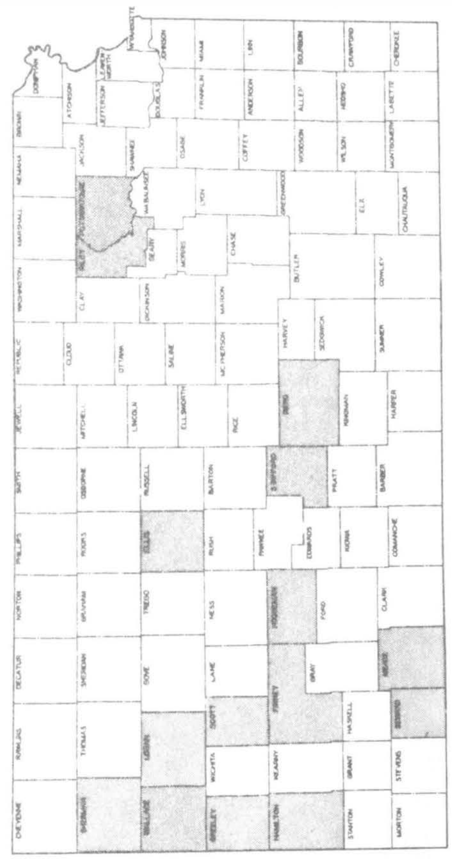
Nebraska Counties

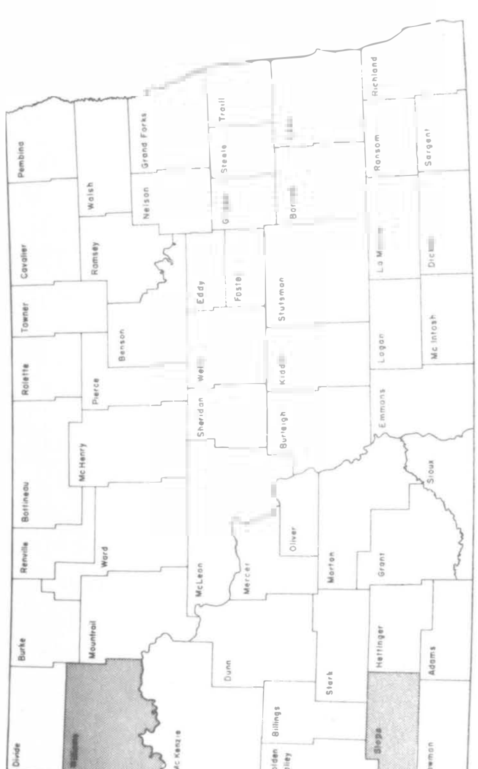
Banner	Dawes	Lincoln	Sioux
Cheyenne	Lancaster	Scotts Bluff	

Kansas Counties

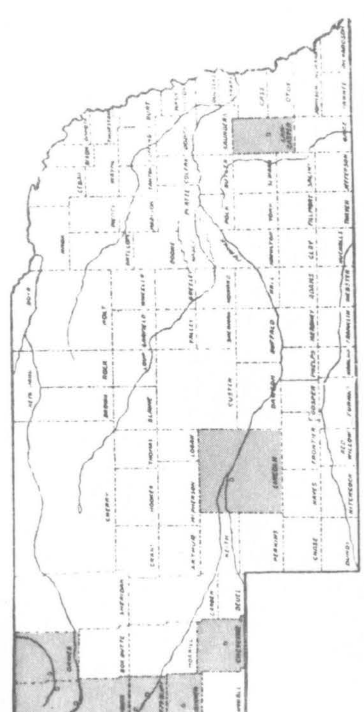
Ellis	Hodgeman	Reno	Sherman
Finney	Logan	Riley	Stafford
Greeley	Meade	Scott	Wallace
Hamilton	Pottawanomie	Seward	







Divide
Burke
Renville
Bottineau
Rolette
Towner
Cavalier
Pembina
Mountrail
Ward
McHenry
Pierce
Ramsey
Walsh
Benson
Nelson
Grand Forks
McKenzie
Dunn
McLean
Sheridan
Eddy
Foster
Stutsman
Steele
Traill
Golden Valley
Billings
Stark
Mercer
Oliver
Burleigh
Morton
Grant
Emmons
Logan
Ransom
Richland
Sargent
Mc Intosh
Sioux
Hettinger
Adams
Bowman



Distribution of *E. hispilabris* in Montana, Oklahoma, Wyoming, and Colorado.

Montana County

Lewis and Clark

Oklahoma Counties

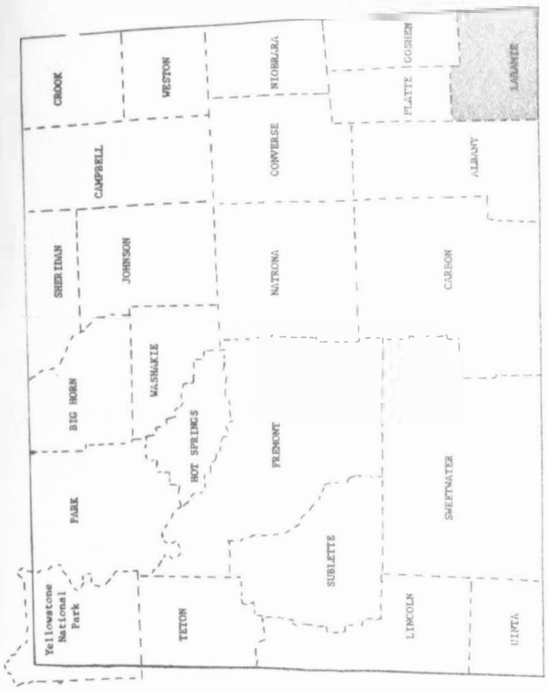
Alfalfa	Cimarron	Oklahoma	Woodward
Beaver	Cleveland	Pawnee	

Wyoming County

Laramie

Colorado Counties

Costilla	Fremont	Las Animas	Otero
Denver	Larimer	Logan	Prowers
El Paso			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GOSHEN
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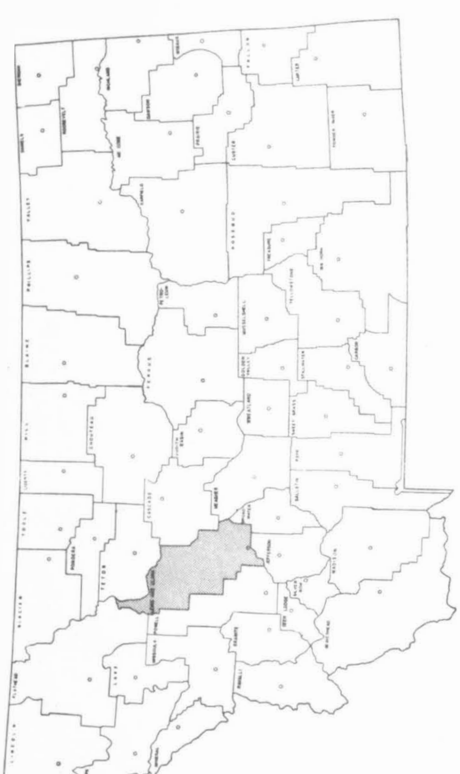
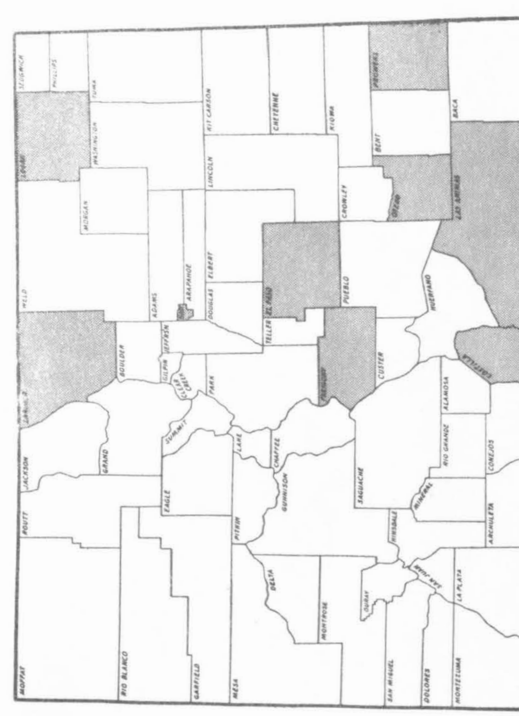
CAMPBELL
CONVERSE
ALBANY
SHERIDAN
JOHNSON
NATRONA
CARBON
BIG HORN
WASHAKIE
HOT SPRINGS
FREMONT
PARK
SUBLETTE
SWEETWATER
Yellowstone National Park
TETON
LINCOLN
UINTA





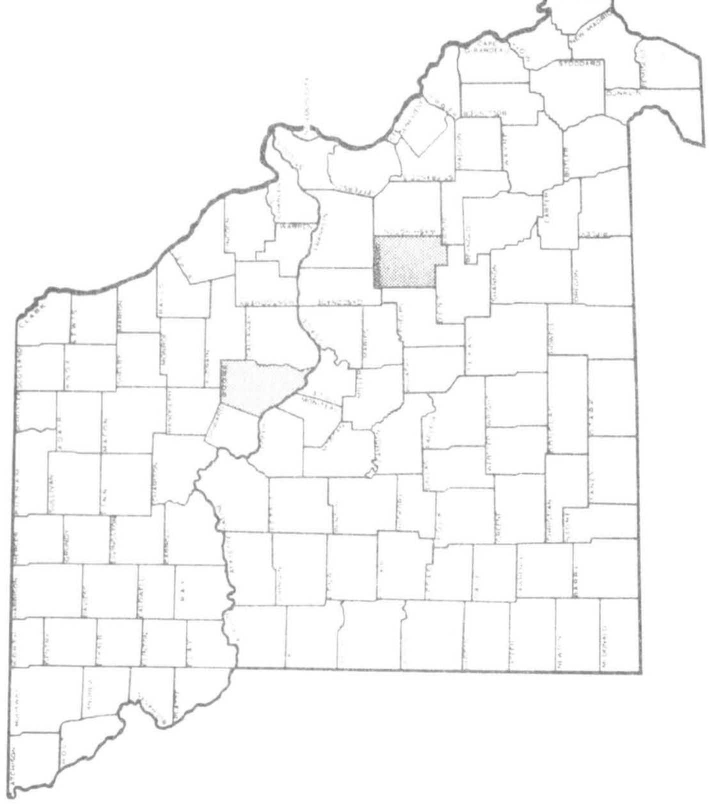
Distribution of *E. tricostata* in Minnesota and Missouri.

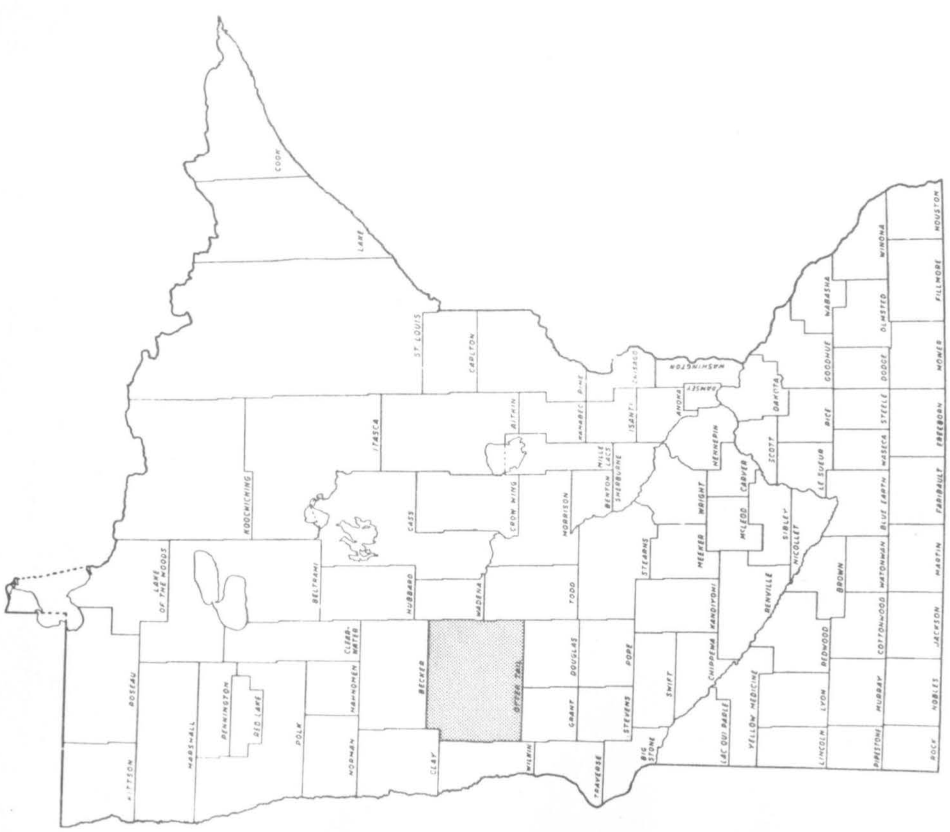
Minnesota County

Ottertail

Missouri Counties

Boone	Crawford




KITTSON
ROSEAU
LAKE OF THE WOODS
MARSHALL
PENNINGTON
RED LAKE
POLK
NORMAN
MAHNOMEN
CLEAR-WATER
BELTRAMI
KOOCHICHING
ITASCA
ST. LOUIS
LAKE
COOK
CARLTON
AITKIN
HUBBARD
CASS
BECKER
CLAY
OTTER TAIL
WADENA
CROW WING
MORRISON
TODD
DOUGLAS
GRANT
WILKIN
TRAVERSE
STEVENS
POPE
BIG STONE
SWIFT
STEARNS
BENTON
SHERBURNE
MILLE LACS
KANABEC
PINE
ISANTI
CHISAGO
ANOKA
WASHINGTON
RAMSEY
HENNEPIN
WRIGHT
MEEKER
KANDIYOHI
CHIPPEWA
LAC QUI PARLE
YELLOW MEDICINE
RENVILLE
MCLEOD
CARVER
SCOTT
DAKOTA
SIBLEY
NICOLLET
LE SUEUR
RICE
GOODHUE
WABASHA
WINONA
OLMSTED
DODGE
STEELE
WASECA
BLUE EARTH
BROWN
REDWOOD
LYON
LINCOLN
PIPESTONE
MURRAY
COTTONWOOD
WATONWAN
MARTIN
FARIBAULT
FREEBORN
MOWER
FILLMORE
HOUSTON
JACKSON
NOBLES
ROCK

Distribution of _E. tricostata_ in North Dakota, South Dakota, Nebraska, and Kansas.

North Dakota Counties

Richland	Walsh

South Dakota Counties

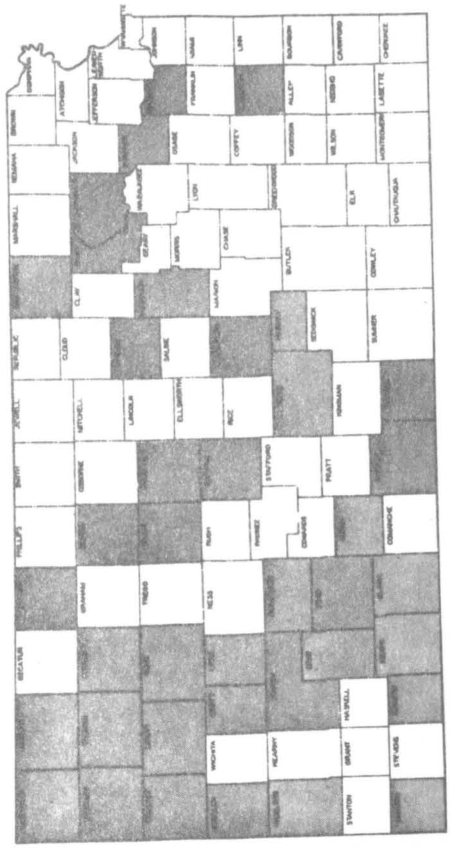
Beadle	Dewey	Jackson	Perkins
Brookings	Faulk	Jerauld	Potter
Brule	Gregory	Jones	Spink
Buffalo	Haakon	Lawrence	Stanley
Custer	Hand	Lyman	Walworth
Day	Harding	Meade	Ziebach
Deuel	Hutchinson	Minnehaha	

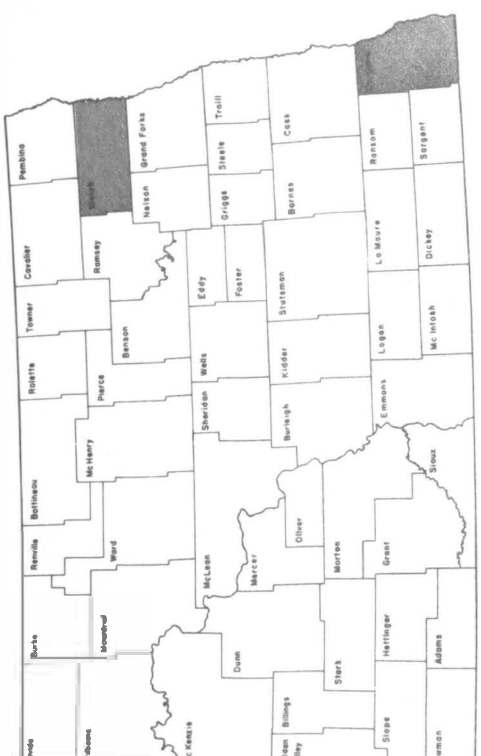
Nebraska Counties

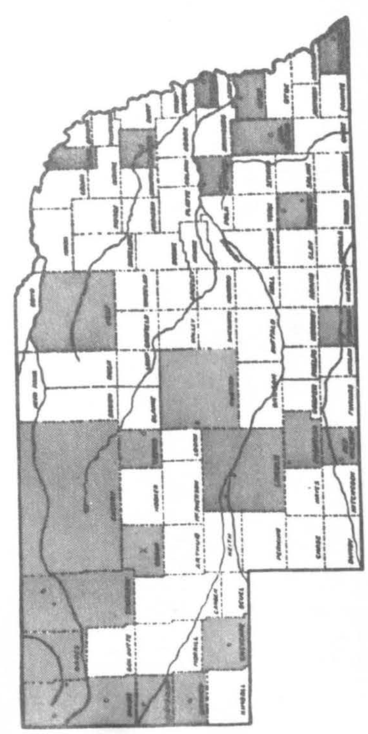
Banner	Custer	Frontier	Richardson
Butler	Dawes	Grant	Scotts Bluff
Cass	Dixon	Holt	Sheridan
Cherry	Douglas	Lancaster	Sioux
Cheyenne	Fillmore	Lincoln	Thomas
Cuming	Franklin	Red Willow	

Kansas Counties

Anderson	Gove	McPherson	Russell
Barber	Gray	Meade	Scott
Barton	Greeley	Morton	Seward
Cheyenne	Hamilton	Norton	Shawnee
Clark	Harper	Ottawa	Sheridan
Dickinson	Harvey	Pottawatomie	Sherman
Douglas	Hodgeman	Rawlins	Thomas
Ellis	Kiowa	Reno	Wallace
Finney	Lane	Riley	Washington
Ford	Logan	Rooks	




Pembina
Cavalier
Towner
Rolette
Bottineau
Renville
Burke
Divide
Williams
Mountrail
Mc Kenzie
Ward
Mc Henry
Pierce
Benson
Ramsey
Nelson
Grand Forks
Traill
Steele
Cass
Griggs
Barnes
Eddy
Foster
Stutsman
Wells
Sheridan
Kidder
Burleigh
McLean
Mercer
Oliver
Morton
Dunn
Billings
Golden Valley
Stark
Slope
Hettinger
Bowman
Adams
Grant
Sioux
Emmons
Logan
Mc Intosh
La Moure
Dickey
Ransom
Sargent



Distribution of _E. tricostata_ in Montana, Wyoming, Colorado, and Oklahoma.

Montana County

Lewis and Clark

Colorado Counties

Denver	Huerfano	Las Animas	Otero
El Paso	Jefferson	Logan	Prowers
Garfield	Larimer		

Oklahoma Counties

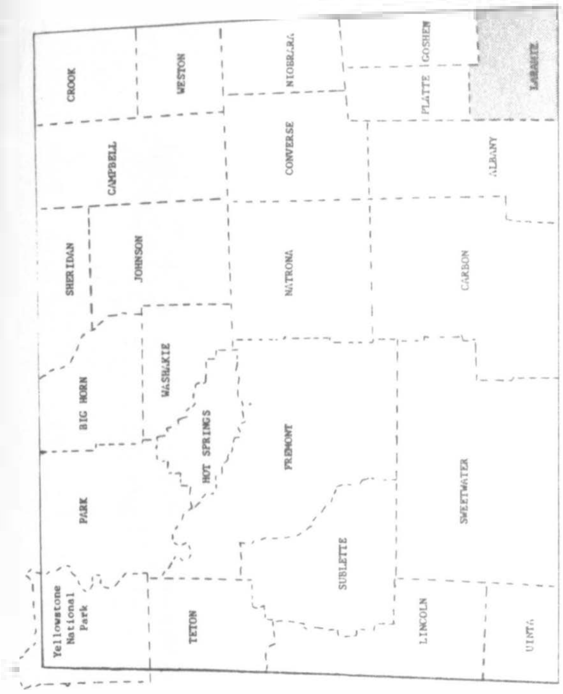
Alfalfa	Cotton	Haskell	Payne
Beaver	Grady	Marshall	Willis
Carter	Grant	Oklahoma	Woodward
Cimarron	Harper		

Iowa Counties

Buchanan	Lyon
Dickinson	Story
Emmet	Woodbury

Wyoming County

Laramie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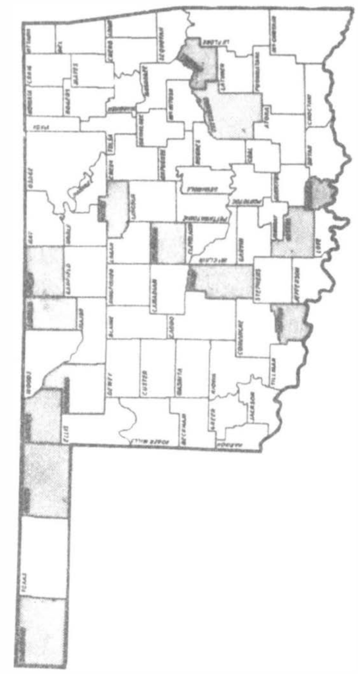
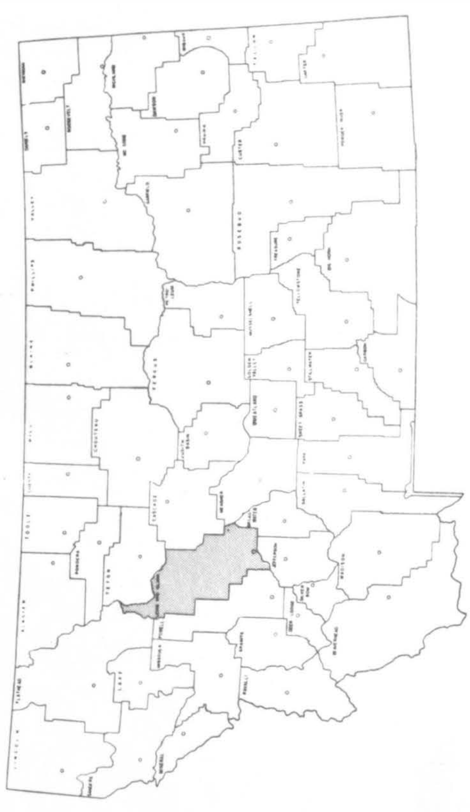
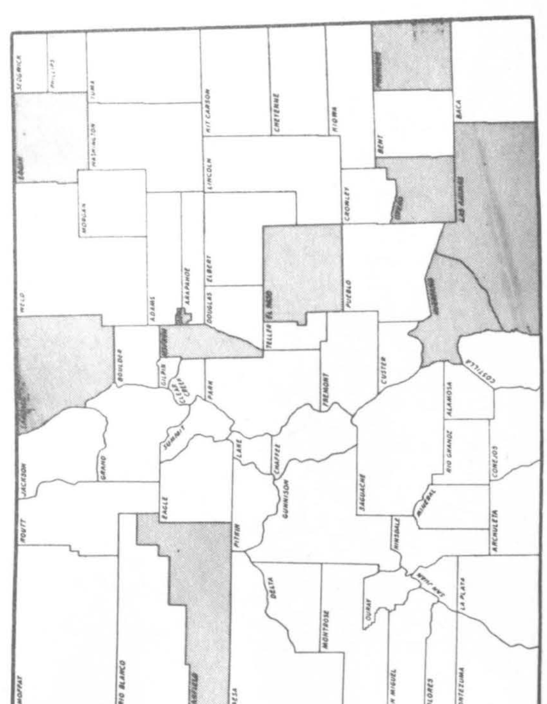
GOSHEN
PLATTE
LARAMIE
CAMPBELL
CONVERSE
ALBANY
SHERIDAN
JOHNSON
NATRONA
CARBON
BIG HORN
WASHAKIE
HOT SPRINGS
FREMONT
PARK
SWEETWATER
SUBLETTE
Yellowstone National Park
TETON
LINCOLN
UINTA



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PHILLIPS
YUMA
LOGAN
WASHINGTON
MORGAN
KIT CARSON
CHEYENNE
KIOWA
BENT
BACA
LINCOLN
CROWLEY
LAS ANIMAS
WELD
ADAMS
ARAPAHOE
DOUGLAS
ELBERT
TELLER
EL PASO
PUEBLO
BOULDER
GILPIN
CLEAR CREEK
PARK
FREMONT
CUSTER
COSTILLA
ALAMOSA
RIO GRANDE
CONEJOS
JACKSON
GRAND
SUMMIT
LAKE
CHAFFEE
SAGUACHE
ROUTT
EAGLE
GUNNISON
MINERAL
ARCHULETA
PITKIN
DELTA
HINSDALE
LA PLATA
MOFFAT
RIO BLANCO
GARFIELD
MESA
MONTROSE
OURAY
SAN MIGUEL
DOLORES
MONTEZUMA

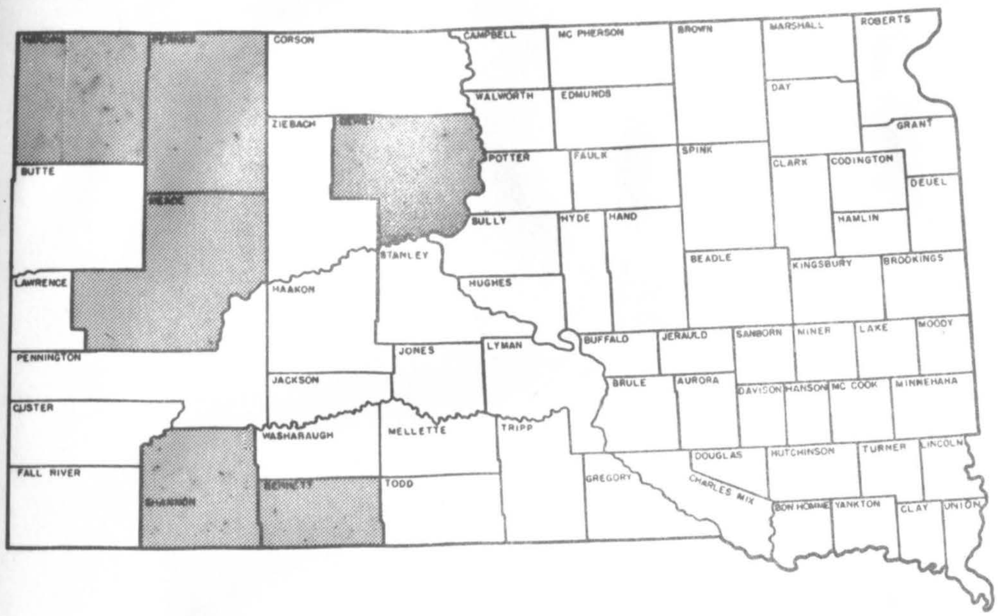
Distribution of _E_. _extricata_ in South Dakota and Nebraska.

South Dakota Counties

Bennett	Meade
Dewey	Perkins
Harding	Shannon

Nebraska Counties

Banner	Garden	Scotts Bluff	Sioux
Cheyenne	Holt	Sheridan	Thomas
Dawes			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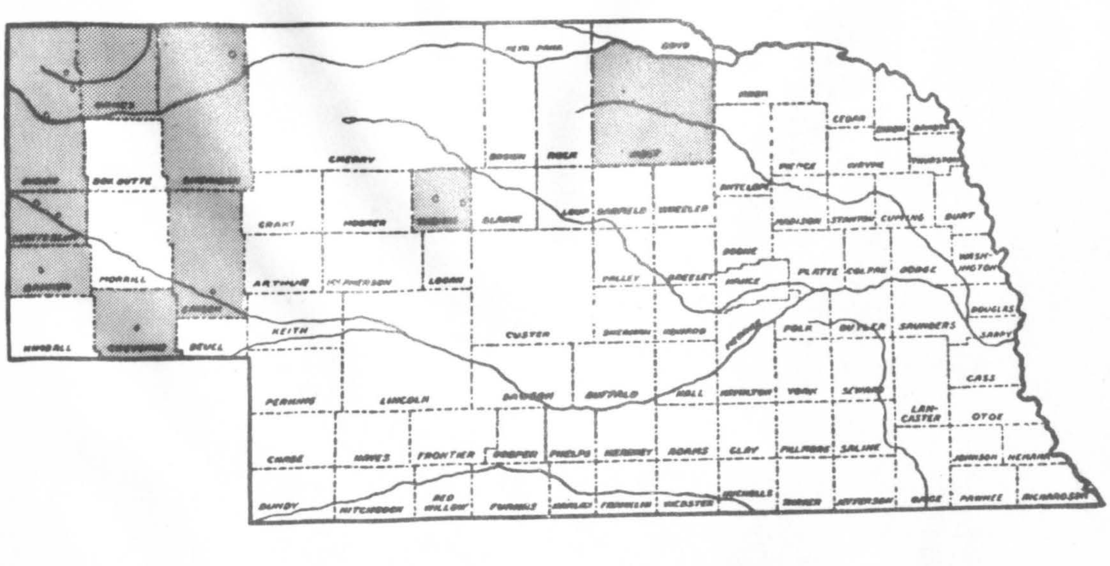
BROWN
MARSHALL
ROBERTS
WALWORTH
EDMUNDS
DAY
GRANT
ZIEBACH
POTTER
FAULK
SPINK
CLARK
CODINGTON
DEUEL
BUTTE
MEADE
SULLY
HYDE
HAND
HAMLIN
STANLEY
BEADLE
KINGSBURY
BROOKINGS
LAWRENCE
HAAKON
HUGHES
BUFFALO
JERAULD
SANBORN
MINER
LAKE
MOODY
PENNINGTON
JONES
LYMAN
JACKSON
BRULE
AURORA
DAVISON
HANSON
MC COOK
MINNEHAHA
CUSTER
WASHABAUGH
MELLETTE
TRIPP
DOUGLAS
HUTCHINSON
TURNER
LINCOLN
FALL RIVER
SHANNON
BENNETT
TODD
GREGORY
CHARLES MIX
BON HOMME
YANKTON
CLAY
UNION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CEDAR
CHERRY
BROWN
ROCK
BOX BUTTE
PIERCE
WAYNE
ANTELOPE
GRANT
HOOKER
BLAINE
LOUP
GARFIELD
WHEELER
MADISON
STANTON
CUMING
BURT
WASH-INGTON
MORRILL
BOONE
ARTHUR
McPHERSON
LOGAN
VALLEY
GREELEY
NANCE
PLATTE
COLFAX
DODGE
DOUGLAS
SARPY
KEITH
CUSTER
SHERMAN
HOWARD
POLK
BUTLER
SAUNDERS
KIMBALL
DEUEL
PERKINS
LINCOLN
DAWSON
BUFFALO
HALL
HAMILTON
YORK
SEWARD
LAN-CASTER
CASS
OTOE
CHASE
HAYES
FRONTIER
GOSPER
PHELPS
KEARNEY
ADAMS
CLAY
FILLMORE
SALINE
JOHNSON
NEMAHA
DUNDY
HITCHCOCK
RED WILLOW
FURNAS
HARLAN
FRANKLIN
WEBSTER
JEFFERSON
GAGE
PAWNEE
RICHARDSON

Distribution of *E. extricata* in Kansas, Wyoming, Oklahoma, and Colorado.

Kansas Counties

Clark	Gove	Kiowa	Riley
Dickinson	Grant	Pottawatomie	Wallace
Finney	Greeley	Reno	

Wyoming Counties

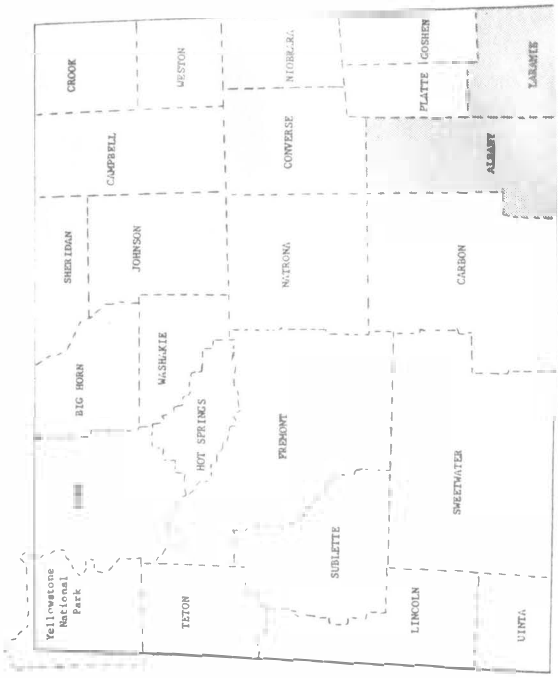
Albany	Laramie

Oklahoma Counties

Beaver	Cimarron	Greer	Harper

Colorado Counties

Chaffee	Huerfano
Denver	Las Animas
El Paso	Logan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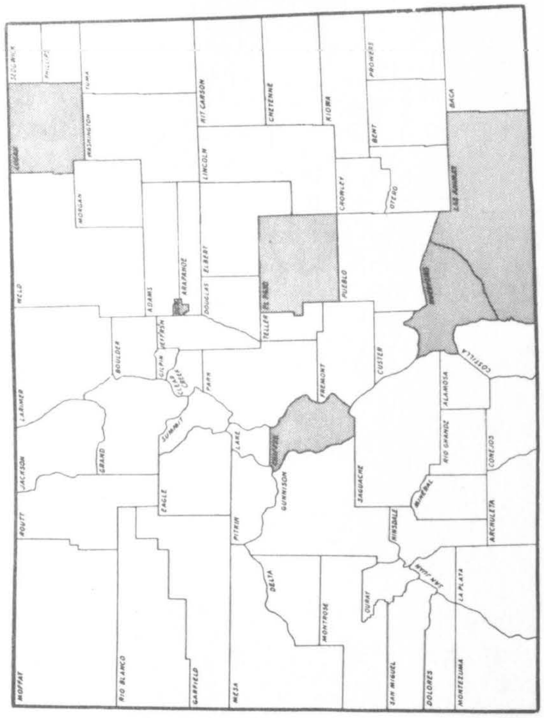
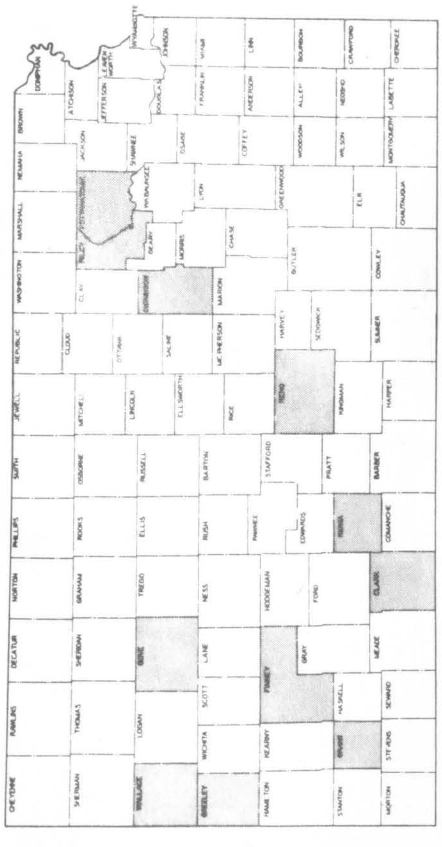
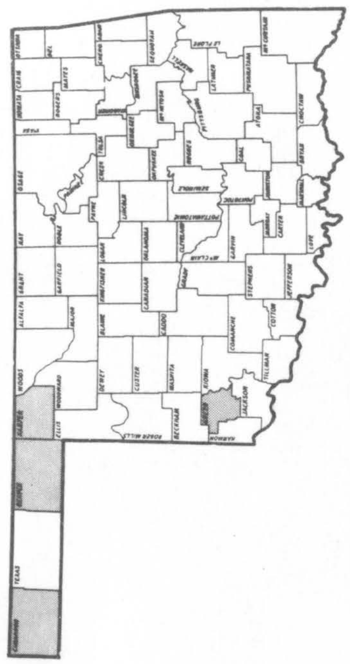
WESTON
NIOBRARA
GOSHEN
PLATTE
LARAMIE
CAMPBELL
CONVERSE
ALBANY
SHERIDAN
JOHNSON
NATRONA
CARBON
BIG HORN
WASHAKIE
HOT SPRINGS
FREMONT
SWEETWATER
SUBLETTE
Yellowstone National Park
TETON
LINCOLN
UINTA







Distribution of *E. obsoleta* in North Dakota, South Dakota, Nebraska, and Kansas.

North Dakota Counties

Slope

South Dakota Counties

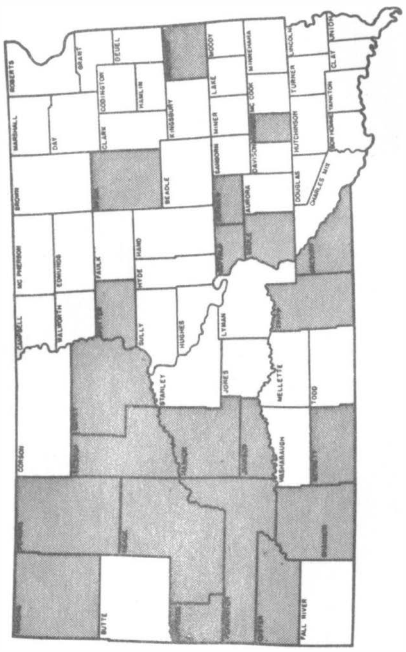
Beadle	Corson	Harding	Spink
Bennett	Day	Lawrence	Sully
Brule	Dewey	Meade	Tripp
Buffalo	Fall River	Perkins	Ziebach
Butte	Haakon	Shannon	

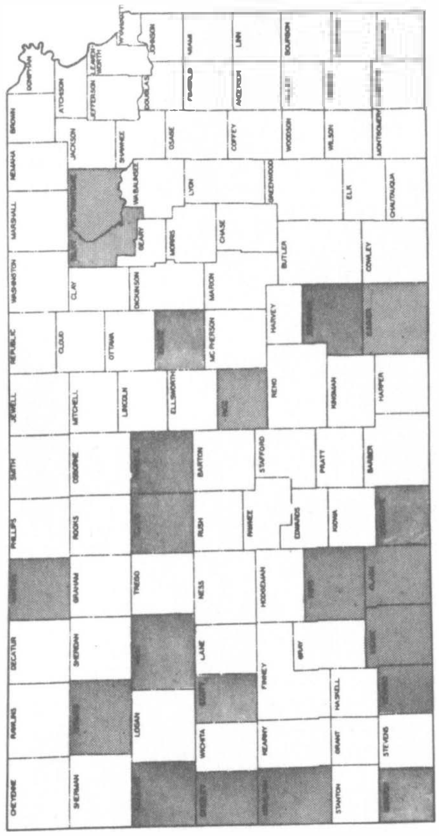
Nebraska Counties

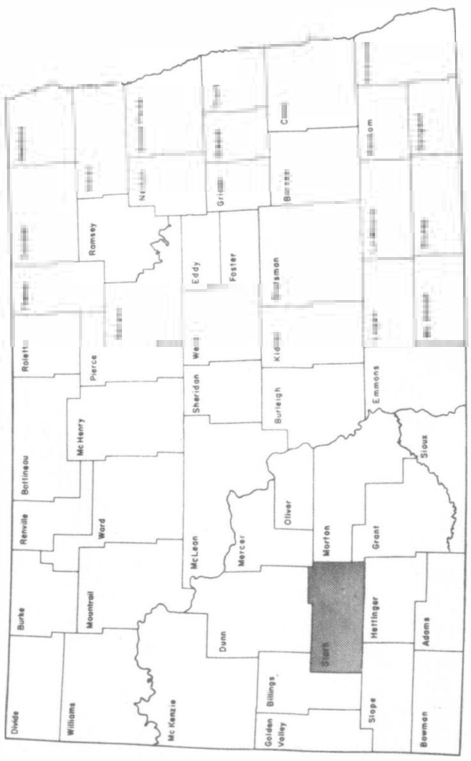
Banner	Dakota	Lancaster	Pine Bluff
Chase	Dawes	Lincoln	Scotts Bluff
Cheyenne	Dundy	Perkins	Sioux

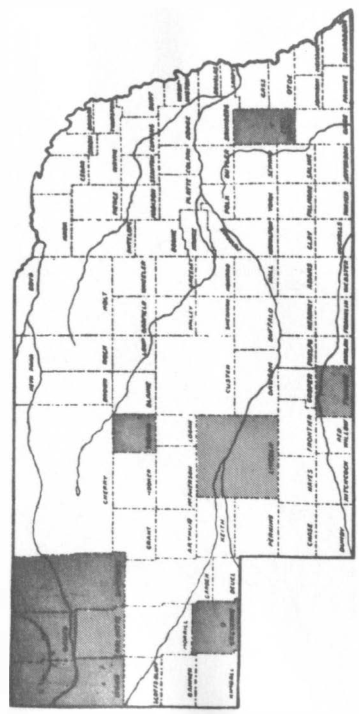
Kansas Counties

Cheyenne	Ford	Logan	Sherman
Clark	Gove	Ness	Stevens
Comanche	Greeley	Scott	Thomas
Ellis	Hamilton	Seward	Wallace
Finney	Harper	Sheridan	









Distribution of *E. obsoleta* in Montana, Wyoming, Colorado, and Oklahoma.

Montana Counties

Custer	Lewis and Clark

Wyoming County

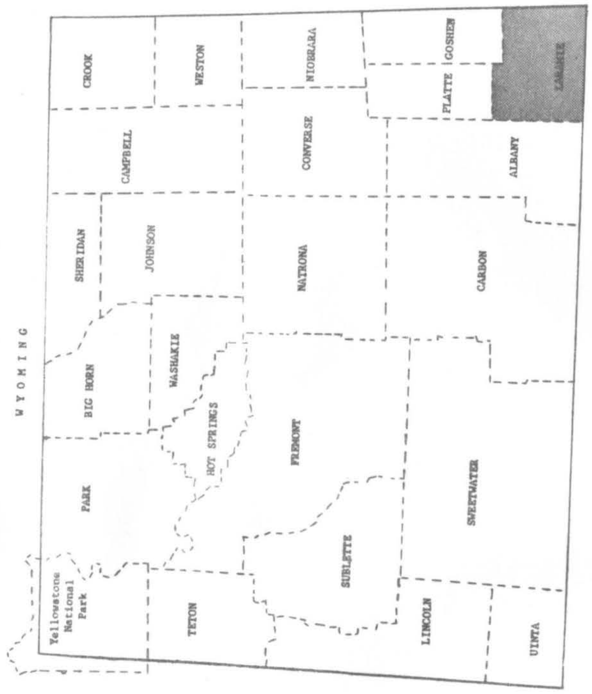
Laramie

Colorado Counties

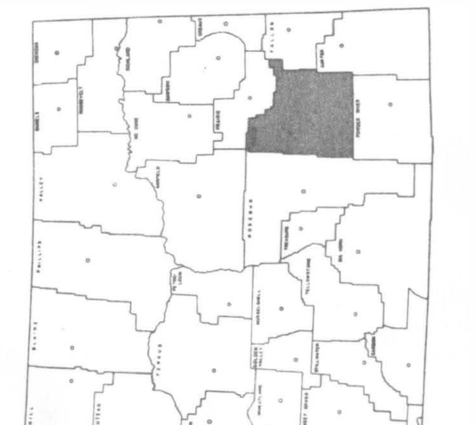
Denver	Jefferson	Logan	Pueblo
El Paso	Las Animas	Mesa	Weld
Fremont	La Plata	Otero	

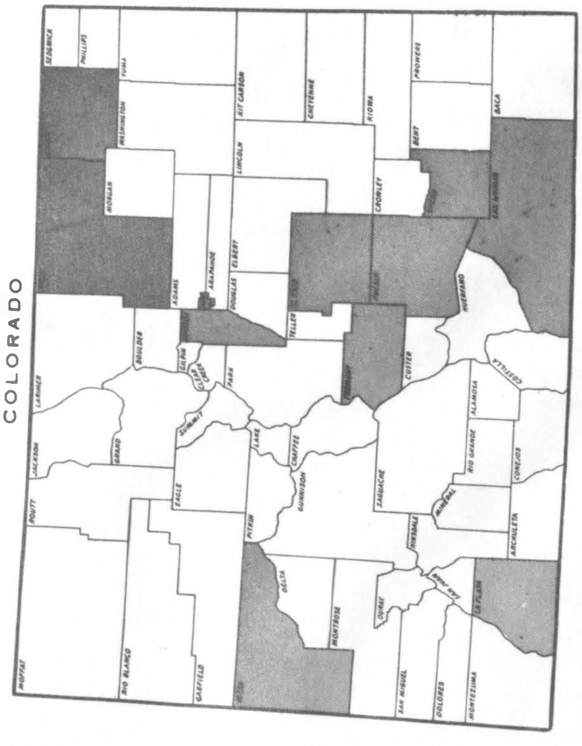
Oklahoma Counties

Cimarron	Woodward
Pawnee	


WYOMING
Yellowstone National Park
PARK
BIG HORN
SHERIDAN
CROOK
CAMPBELL
JOHNSON
WASHAKIE
HOT SPRINGS
FREMONT
NATRONA
CONVERSE
WESTON
NIOBRARA
GOSHEN
PLATTE
LARAMIE
ALBANY
CARBON
SWEETWATER
SUBLETTE
TETON
LINCOLN
UINTA


OKLAHOMA


MONTANA


COLORADO
SEDGWICK
PHILLIPS
YUMA
WASHINGTON
MORGAN
KIT CARSON
CHEYENNE
KIOWA
PROWERS
BENT
BACA
LINCOLN
ELBERT
ADAMS
ARAPAHOE
DOUGLAS
TELLER
CROWLEY
CUSTER
HUERFANO
LAS ANIMAS
COSTILLA
ALAMOSA
CONEJOS
RIO GRANDE
ARCHULETA
LA PLATA
MONTEZUMA
DOLORES
SAN MIGUEL
OURAY
MONTROSE
DELTA
GARFIELD
RIO BLANCO
MOFFAT
ROUTT
JACKSON
LARIMER
BOULDER
GRAND
GILPIN
CLEAR CREEK
SUMMIT
EAGLE
PITKIN
LAKE
CHAFFEE
GUNNISON
SAGUACHE
HINSDALE
MINERAL
PARK

Distribution of *Embaphion muricatum* in North Dakota, South Dakota, Nebraska, and Kansas.

North Dakota County

Stark

South Dakota Counties

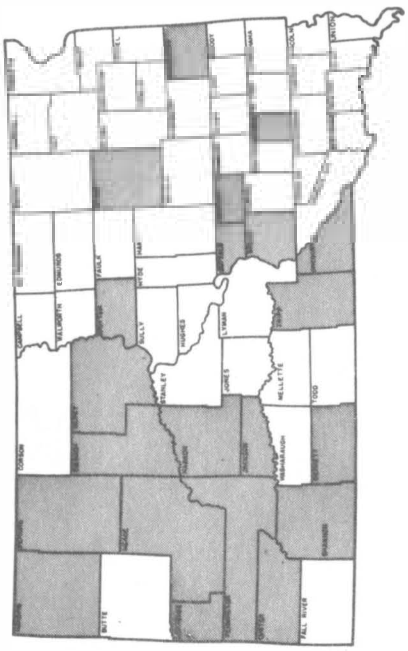
Bennett	Gregory	Jerauld	Potter
Brookings	Haakon	Lawrence	Shannon
Brule	Hanson	Meade	Spink
Buffalo	Harding	Pennington	Tripp
Custer	Jackson	Perkins	Ziebach
Dewey			

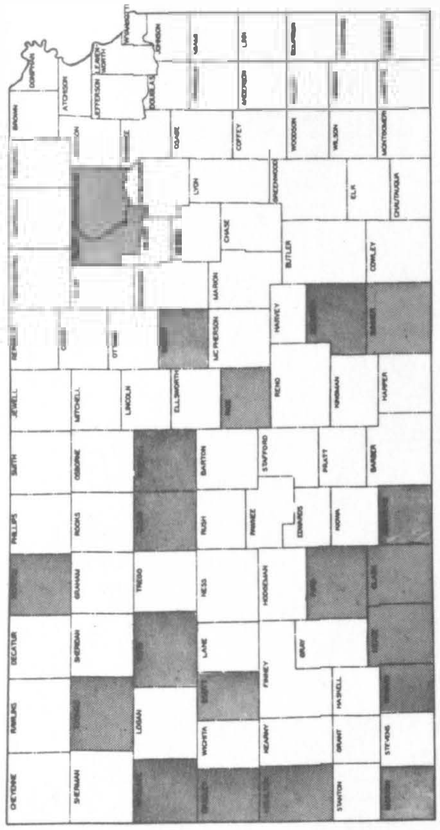
Nebraska Counties

Box Butte	Furnas	Lincoln	Sioux
Cheyenne	Lancaster	Sheridan	Thomas
Dawes			

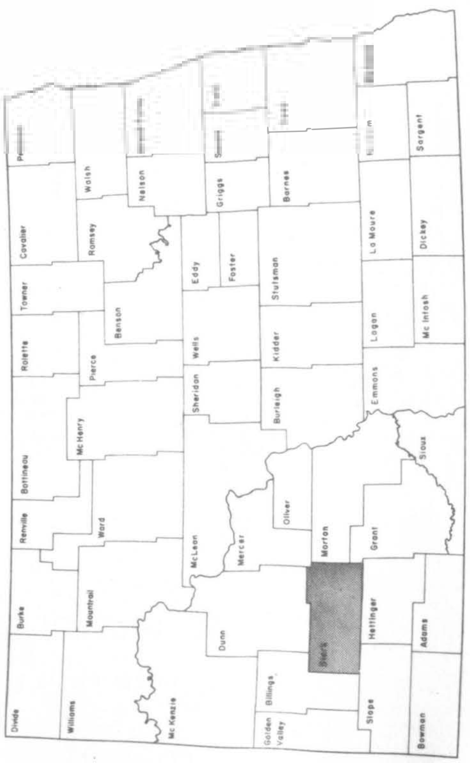
Kansas Counties

Clark	Hamilton	Rice	Sedgwick
Comanche	Meade	Riley	Seward
Ellis	Morton	Russel	Sumner
Ford	Norton	Saline	Thomas
Gove	Pottawatomie	Scott	Wallace
Greeley			





CHEYENNE
RAWLINS
DECATUR
PHILLIPS
SMITH
JEWELL
SHERMAN
SHERIDAN
GRAHAM
ROOKS
OSBORNE
MITCHELL
LINCOLN
ELLSWORTH
LOGAN
TREGO
RUSH
BARTON
WICHITA
LANE
NESS
PAWNEE
STAFFORD
RENO
HARVEY
MC PHERSON
MARION
CHASE
LYON
OSAGE
COFFEY
WOODSON
WILSON
MONTGOMERY
ELK
CHAUTAUQUA
COWLEY
BUTLER
GREENWOOD
KINGMAN
HARPER
PRATT
BARBER
KIOWA
EDWARDS
HODGEMAN
FINNEY
GRAY
HASKELL
GRANT
STANTON
STEVENS
KEARNY
CLARK
ANDERSON
LINN
MIAMI
JOHNSON
DOUGLAS
JEFFERSON
ATCHISON
DONIPHAN
BROWN



Divide
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Mc Kenzie
Golden Valley
Billings
Slope
Bowman
Burke
Mountrail
Dunn
Stark
Hettinger
Adams
Renville
Ward
McLean
Mercer
Morton
Grant
Bottineau
McHenry
Sheridan
Oliver
Rolette
Pierce
Wells
Burleigh
Sioux
Towner
Benson
Eddy
Kidder
Emmons
Cavalier
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Foster
Stutsman
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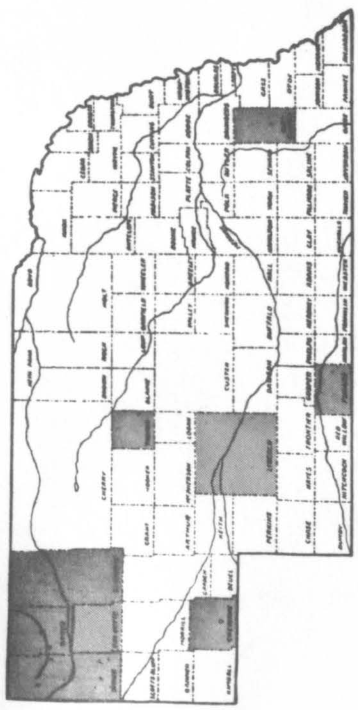
Nelson
Griggs
Barnes
La Moure
Dickey
Sargent



CHERRY
LOGAN
LINCOLN
PERKINS
CHASE
HAYES
FRONTIER
KEITH
CUSTER
BUFFALO
DAWSON

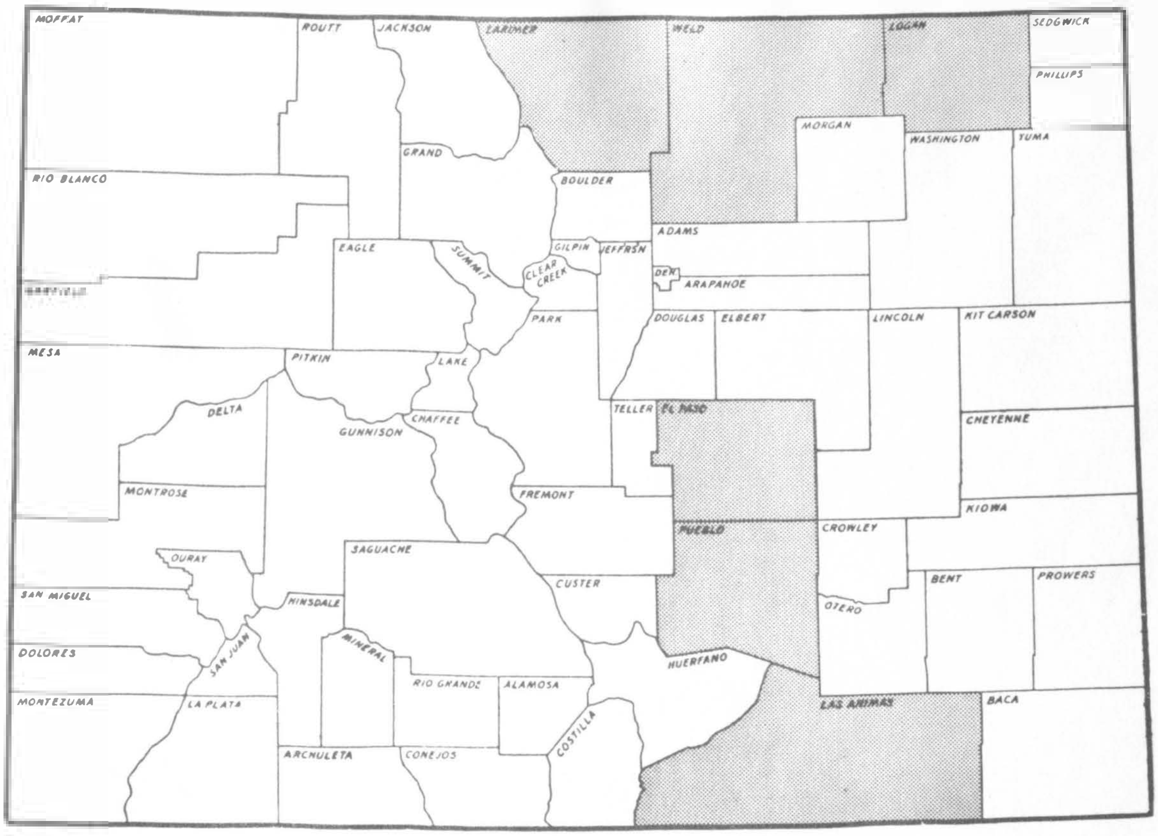
Distribution of _E. muricatum_ in Colorado and Oklahoma.

Colorado Counties

El Paso	Logan
Larimer	Pueblo
Las Animas	Weld

Oklahoma Counties

Cimarron	Payne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JACKSON
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WELD
LOGAN
SEDGWICK
PHILLIPS
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WASHINGTON
YUMA
GRAND
BOULDER
RIO BLANCO
ADAMS
EAGLE
SUMMIT
GILPIN
JEFFRSN
CLEAR CREEK
DEN
ARAPAHOE
PARK
DOUGLAS
ELBERT
LINCOLN
KIT CARSON
MESA
PITKIN
LAKE
DELTA
TELLER
EL PASO
CHEYENNE
CHAFFEE
GUNNISON
FREMONT
MONTROSE
KIOWA
PUEBLO
CROWLEY
OURAY
SAGUACHE
CUSTER
BENT
PROWERS
SAN MIGUEL
HINSDALE
OTERO
DOLORES
MINERAL
SAN JUAN
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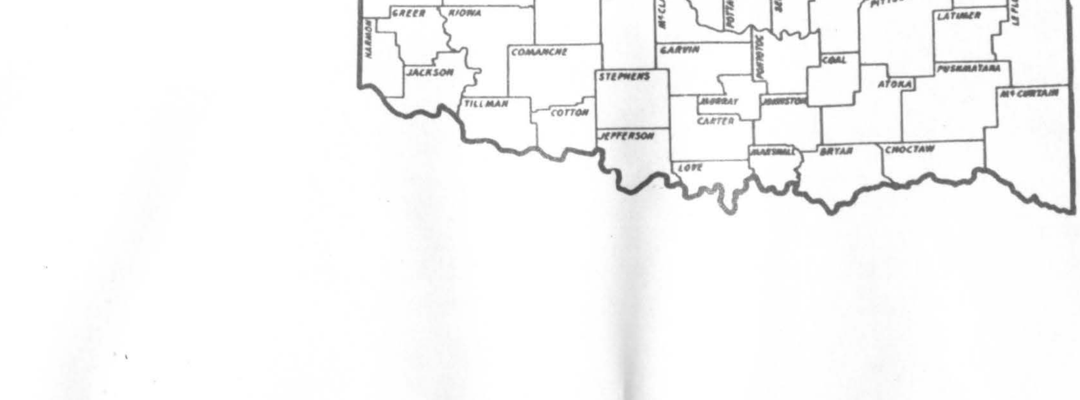
CONEJOS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HARPER
WOODS
ALFALFA
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KAY
OSAGE
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CRAIG
OTTAWA
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MAJOR
GARFIELD
NOBLE
ROGERS
MAYES
DEWEY
BLAINE
KINGFISHER
LOGAN
CREEK
TULSA
CHERO
ADAIR
LINCOLN
CUSTER
CANADIAN
OKLAHOMA
OKMULGEE
SEQUOYAH
ROGER MILLS
CADDO
OKFUSKEE
MCINTOSH
BECKHAM
WASHITA
GRADY
CLEVELAND
POTTAWATOMIE
SEMINOLE
HUGHES
PITTSBURG
HASKELL
GREER
KIOWA
MCCLAIN
LATIMER
LE FLORE
HARMON
COMANCHE
GARVIN
PONTOTOC
COAL
JACKSON
STEPHENS
MURRAY
ATOKA
PUSHMATAHA
TILLMAN
COTTON
CARTER
JOHNSTON
MCCURTAIN
JEFFERSON
LOVE
MARSHALL
BRYAN
CHOCTAW

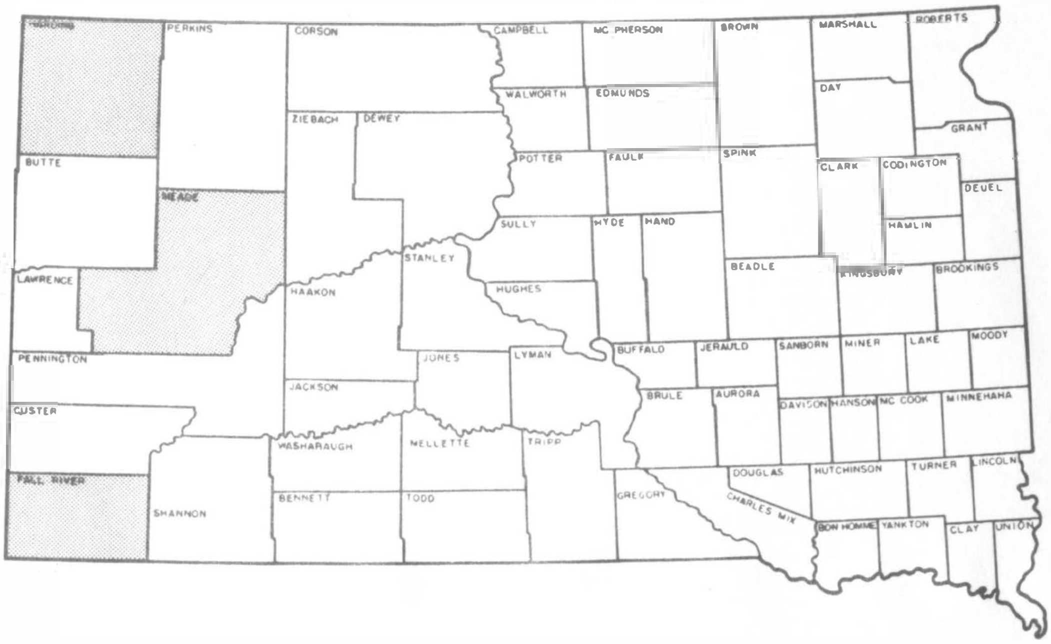
Distribution of *Glyptasida sordida* in South Dakota and Nebraska.

South Dakota Counties

Fall River	Meade
Harding	

Nebraska Counties

Banner	Red Willow
Cheyenne	Sioux
Dawes	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MARSHALL
ROBERTS
WALWORTH
EDMUNDS
DAY
GRANT
ZIEBACH
DEWEY
POTTER
FAULK
SPINK
CLARK
CODINGTON
DEUEL
BUTTE
MEADE
SULLY
HYDE
HAND
HAMLIN
STANLEY
LAWRENCE
HAAKON
HUGHES
BEADLE
KINGSBURY
BROOKINGS
PENNINGTON
JONES
LYMAN
BUFFALO
JERAULD
SANBORN
MINER
LAKE
MOODY
JACKSON
BRULE
AURORA
DAVISON
HANSON
MC COOK
MINNEHAHA
CUSTER
WASHABAUGH
MELLETTE
TRIPP
DOUGLAS
HUTCHINSON
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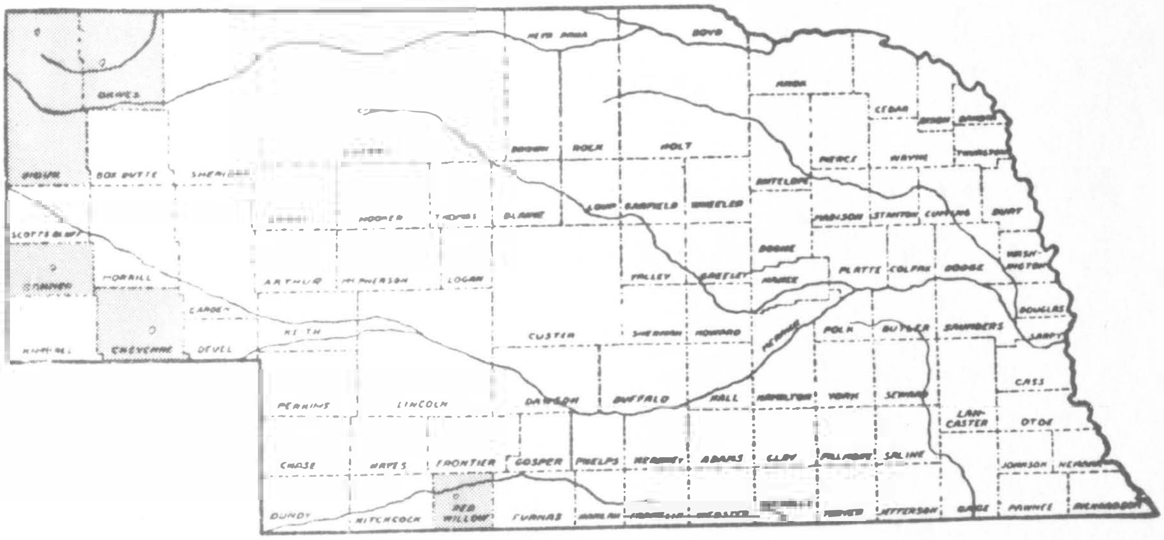
SHANNON
BENNETT
TODD
GREGORY
CHARLES MIX
BON HOMME
YANKTON
CLAY
UNION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BOX BUTTE
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MORRILL
KIMBALL
CHEYENNE
DEUEL
GARDEN
KEITH
ARTHUR
MC PHERSON
LOGAN
HOOKER
THOMAS
BLAINE
LOUP
GARFIELD
WHEELER
ROCK
HOLT
BOYD
KNOX
CEDAR
PIERCE
WAYNE
ANTELOPE
MADISON
STANTON
CUMING
BURT
BOONE
PLATTE
COLFAX
DODGE
WASH-INGTON
VALLEY
GREELEY
NANCE
CUSTER
SHERMAN
HOWARD
MERRICK
POLK
BUTLER
SAUNDERS
DOUGLAS
SARPY
CASS
PERKINS
LINCOLN
DAWSON
BUFFALO
HALL
HAMILTON
YORK
SEWARD
LAN-CASTER
OTOE
CHASE
HAYES
FRONTIER
GOSPER
PHELPS
ADAMS
CLAY
SALINE
JOHNSON
DUNDY
HITCHCOCK
RED WILLOW
FURNAS
JEFFERSON
GAGE
PAWNEE
RICHARDSON

Distribution of <u>Asidopsis opaca</u> in South Dakota, Nebraska, and Oklahoma.

<u>South Dakota Counties</u>

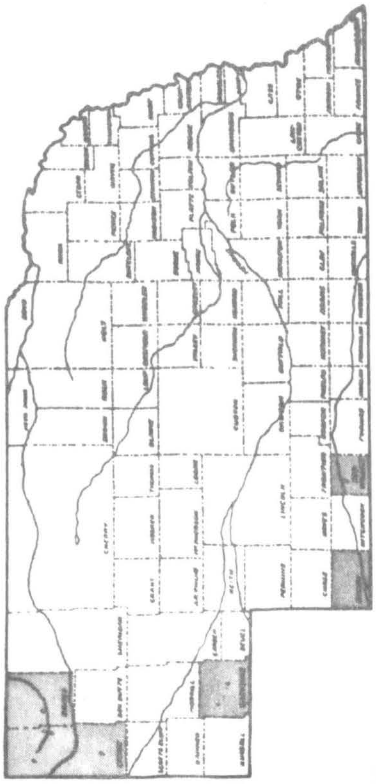
Fall River	Meade
Harding	

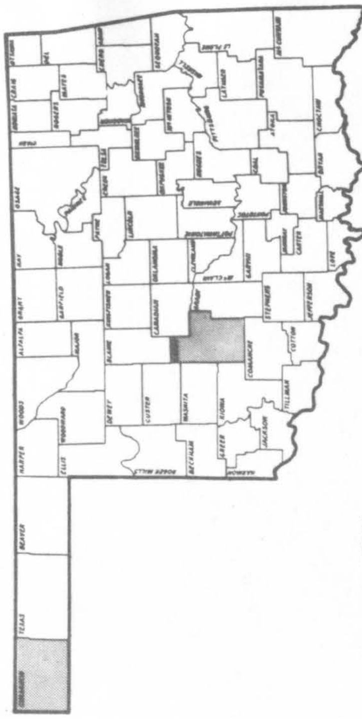
<u>Nebraska Counties</u>

Cheyenne	Red Willow
Dawes	Sioux
Dundy	

<u>Oklahoma Counties</u>

Caddo	Cimarron





OKLAHOMA

Distribution of *A. polita* in South Dakota, Nebraska, and Oklahoma.

South Dakota Counties

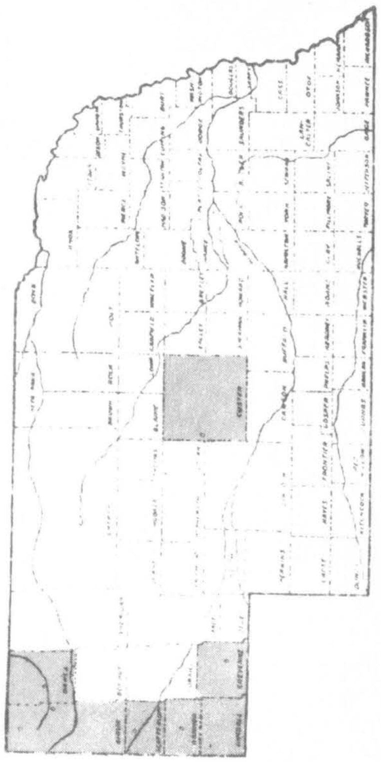
Fall River	Harding

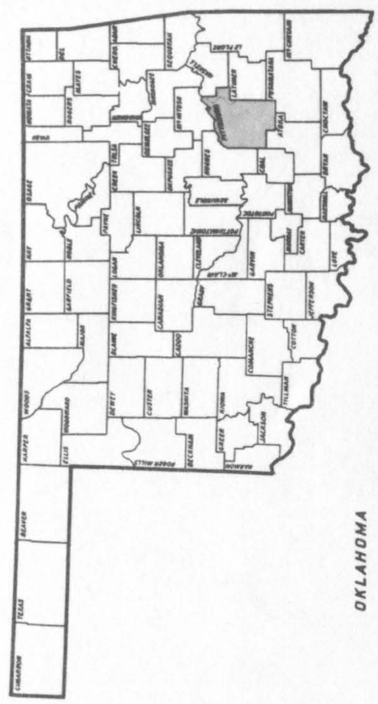
Nebraaska Counties

Banner	Custer	Kimball	Sioux
Cheyenne	Dawes	Scotts Bluff	

Oklahoma County

Pittsburg





OKLAHOMA